The evolution of the cemented habit in the bivalved molluscs

Thesis

THE EVOLUTION OF THE CEMENTED HABIT IN THE BIVALVED MOLLUSCS

A thesis submitted for the Degree of Doctor of Philosophy

by

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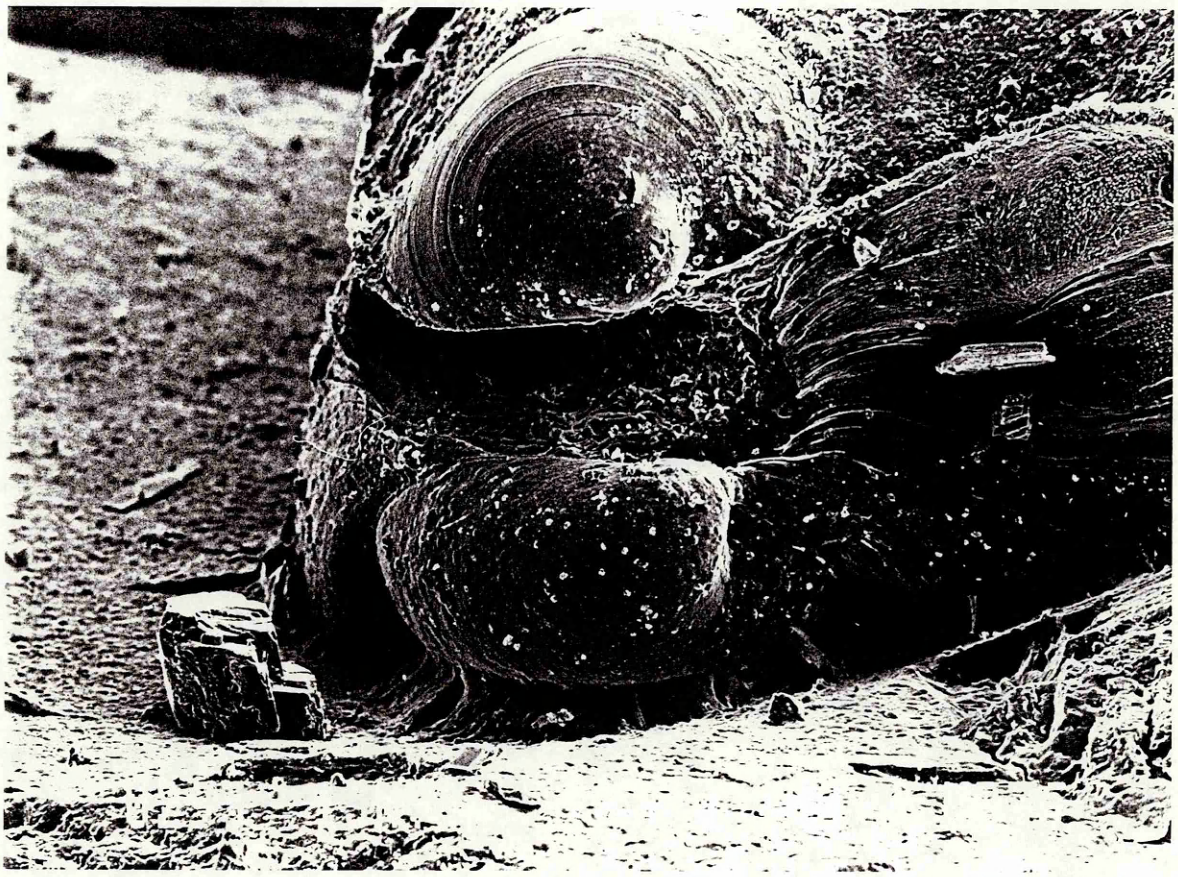

Frontispiece: The Pacific oyster, *Crassostrea gigas*, six weeks after initial settlement, attached to a calcite rhomb.

For J

Get better soon

ABSTRACT

The ability to cement to a hard substratum has evolved repeatedly in the bivalved molluscs. Twenty clades of cementing bivalves have been identified from a broad range of bivalve taxa. Such polyphyletic acquisition of the habit raises a number of questions concerning the preadaptations which allow bivalves to cement and the selection pressures which favour this mode of attachment.

Detailed examination of cementation in members of the Ostreidae reveals that a calcareous extra-periostracal cement is responsible for attachment. Spherulitic growth of cement, whose composition is identical to that of the shell layers, results in structures reminiscent of diagenetic cements. These observations suggest that extrapallial fluid 'leaks' through a permeable periostracum; resulting in precipitation of calcium carbonate between the periostracum and the substratum. Similar observations are made for most other living shell cementing bivalves, implying a convergence of mechanism. The only exception are the chamids which appear to utilise a weaker organic bond. Less than 10% of fossil Chamacea are preserved attached to their substrata, suggesting that this weaker mode of attachment has been employed in this superfamily throughout its evolutionary history.

Having established a common mechanism by which most bivalves cement it is possible to suggest the possible preadaptations. Principal requirements are the possession of a thin and 'leaky' periostracum, a highly extensible mantle edge and a suitable life orientation. Indeed, most cementing bivalves have evolved from pleurothetic byssate stock. The Pectinidae, in which the cemented habit has evolved at least four times, are shown to possess these key preadaptations.

Mytiloids have never cemented despite having members which have dwelt on hard substrates since the Ordovician. Examination of modern Mytilacea suggests that the group lacks all the fundamental preadaptations for cementation.

There is little evidence to support the traditional view that cementation is an adaptation to life in a high energy environment. The independent appearance of many of the cementing clades during the early Mesozoic coincides with the increased predation

pressure which has been documented for that time. A causal link is implied by experimental work: predators display a significant preference for more easily manipulated byssate prey.

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Peter Skelton supervised this project. My thanks go to him for letting me go my own way while at the same time showing a great amount of enthusiasm. He also bought me a cluster of *Lopha* and taught me to spell occurrence.

Dealing with so many clades of cementing bivalves is rather like trying to hold a hand of cards when your hands are too small. Solene and Noel Morris, John Taylor and Tim Palmer have all provided an immense amount of help and advice. Many others have also lent and donated specimens, for which I am grateful. In particular I should thank all the curators of the various museums I have visited for their help.

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Naomi Williams assisted with SEM work at the OU, whilst JohnTaylor and Nadine Wilmot generously allowed me to use the facilities at The Natural History Museum when the OU machine was down.

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Camp drew figures 6.7 and 6.8 with her usual flare. Many thanks also to Clive Oppenheimer who stayed up tonight to help with the photocopying and to keep me awake.

My final thanks must go to J for everything.

A NOTE ON PHOTOGRAPHY

On returning from the Malacological Congress in Tübingen in August 1989 I discovered that several hundred negatives had been stolen, amongst other things, from my office. Of these an estimated two hundred and fifty were important in this thesis, either as illustrations, or more importantly as a source of data. The Open University made financial provision for the replacement of this material and the time that this required, for which I am grateful. However, much was simply irreplaceable. Not only do soft part preparations deteriorate over time but also many of the negatives illustrated specimens in the Ivö Klack collection in Copenhagen, experimental procedures in Oban and wild material in Galway Bay. It has, therefore, been necessary to replace some of these for reproduction in this thesis by making new negatives from contact prints of the originals or from colour slides. Consequently the quality of some of the photographs in this thesis are poorer than might be hoped. The figures which have suffered in this way are clearly marked.

CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

The bivalved molluscs pursue a remarkably diverse range of life habits. The extreme morphological plasticity of the bivalve body plan has enabled them to exploit both infaunal and epifaunal niches (see Figure 1.1).

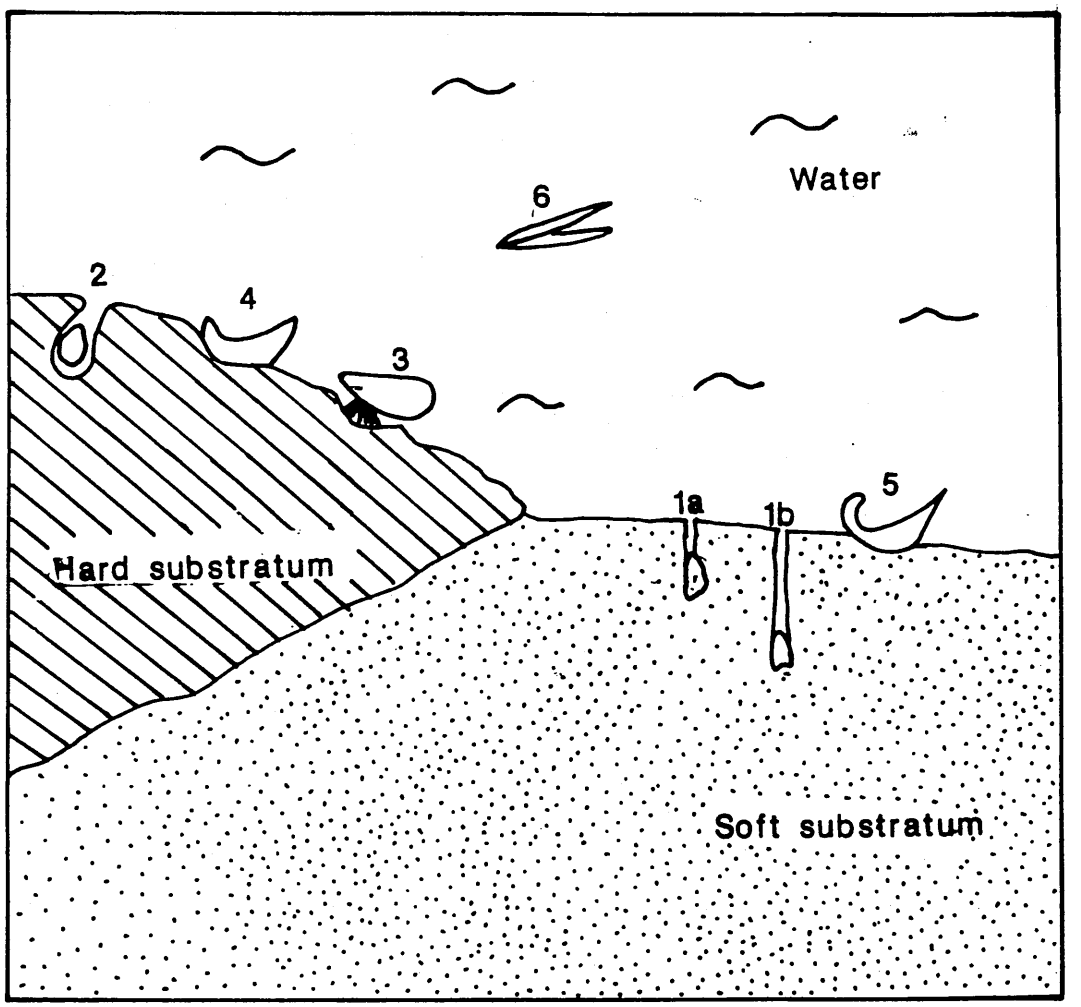


Figure 1.1: The different life habits exploited by the Bivalvia, after Stanley (1970). 1= Burrowing, (a)-shallow and (b)-deep; 2=Boring; 3=Byssate; 4=Cemented; 5=Reclining and 6=Swimming. Stanley's seventh group, nestlers, is not distinguished in this thesis, its members being classed as byssate.

Such adaptability has led the bivalves into spectacular radiations over evolutionary time which, coupled with their excellent fossil record (see Raup, 1979), has made them

frequent subjects of functional morphology studies. One such study is that of Stanley (1970), a classic investigation into the relationship between shell morphology and life habit of the bivalves of east coast America. Stanley recognises the following modes of life in bivalves:

Burrowing: The vast majority of bivalves are infaunal, burrowing into soft sediments to varying depths. This is considered the most primitive life mode and indeed the habit has been retained by bivalves considered to be the amongst the least derived, e.g. Nuculoida. However, the habit also encompasses the more 'advanced' deep-burrowing siphonate taxa, e.g. heteroconchs.

Byssate: Yonge (1962b) notes that most, if not all, larval bivalves adhere to the substrate by means of tough, flexible proteinaceous byssus threads secreted by the foot. This attachment mode has been neotenously retained in a large number of adult bivalves. Attachment by this means may be either to soft or hard substrates and these are distinguished by the terms endo- and epibyssate. Exposed byssate taxa are those which do not display a marked preference for crevices. Adult byssate taxa include most mytiloids and arcoids.

Cemented: Firm attachment, usually by one valve, to a hard substratum such that the bond does not sunder readily upon death. The habit is epitomised by the oysters.

Recliners: No firm attachment to a substrate. The bivalve rests on one or both of the valves, usually on soft substrata. Examples of reclining taxa, which rest on one valve, include many of the the Gryphaeidae, and the anomiid *Placuna*. Recumbent rudists lay on both valves.

Swimming: Swimming by either valve clapping, tentacular movements or both, e.g. *Lima* and *Pecten maximus*.

Boring: Living encased in hard substrata in crypts of their own making. The crypts are formed by physical abrasion, chemical attack, or a combination of the two. The boring habit is employed by the lithophagid mytilids and members of the Pholadacea.

Nestling: Living in excavations within a hard substrate, usually attached by a byssus. Distinction is made between the boring and nestling bivalves by the latter's

inability to make its own excavation. Nicol (1983) reviews the criteria as to what does and does not constitute a nestling bivalve. In this thesis bivalves which nestle have been categorised as byssate in order to avoid such arguments.

The habits defined above may not be considered mutually exclusive. Life habit may change over ontogeny, for example *Chlamys pusio* is byssally attached early in life, cementing later. Others may alternate; many of the scallops are free living recliners e.g. *Chlamys opercularis*, or are byssally attached e.g. *Placopecten magellanicus*, but also possess the ability to swim.

Skelton et al. (1990) investigate the post-Palaeozoic radiation of the bivalves. By plotting the changing occupancy of ten autecological categories over geological time they outlined the decline in the exposed byssate taxa and the radiation of the more 'advanced' life habits. It is the study of one of these radiations which is the subject of this thesis: the evolution of attachment by cementation to hard substrata.

1.2 THE CEMENTED BIVALVES

The definition of cementation which I have used in this thesis is that of firm fixation to a hard substratum which persists after death of the organism. The substratum must be a separate entity, thus ruling out members of the Clavagellacea (see 2.3.4.3).

Two modes of cementation are recognised in both living and fossil material. The vast majority adhere by fixation of the surface of one valve to a hard substratum, such that the morphology of that valve closely follows the substrate topography. Members of the Anomiacea differ in that both valves remain free but the organism attaches by a calcareous plug, actually a modified byssus, which is firmly fixed to the substratum. This firm attachment, which persists after death, fulfils the definition of cementation.

Cementation is an advanced life habit requiring considerable modification to the organization of the bivalve and posing a number of problems associated with immobility. The earliest known cemented bivalve is the pseudomonotid *Pachypteria* from the Viséan (Carboniferous). Despite this and a small number of Permian

examples from the same family (Newell and Boyd, 1970) it is not until the Mesozoic that the habit appears in a large number of unrelated taxa.

According to Nicol (1978) only 3% of extant bivalve species possess the ability to cement. Yet of the limited number of taxa, both living and extinct, which have evolved cementation, many are amongst the most successful and widespread of bivalves; consider, for example, the oysters and the extinct Hippuritacea (rudists).

The evolution of cementation in the Bivalvia is polyphyletic; the habit has been evolved independently in a number of unrelated groups (see Chapter 2). This convergence of habit is immediately arresting. The implication of its repeated evolution is that (i) there is, in certain circumstances, a definite selective advantage in cementation, and (ii) that the habit is a very simple adaptation which may be easily attained.

Study of the evolution of this interesting phenomenon is, however, hampered by the convergence of form that these bivalves display, such as monomyarianism and general valve morphology. Gross morphological distortion of the valves because of attachment to irregular substrata tends to mask the true identity of many of the forms. This is compounded by the erroneous belief that most cementing bivalves are merely oysters or oyster-like bivalves. As a result, attempts to discover the relationships of many of the cementing bivalves, in particular to identify the origins of the true oysters, have excited much debate, e.g. Newell and Boyd (1970), Yonge (1979), Stenzel (1971), Nicol (1984) and Newell and Boyd (1989).

The crux of the problem lies with our lack of understanding about the cementation process. It is necessary to establish how cementation occurs so that we can make predictions about the anatomical requirements for cementation and also understand the effects of cementation on bivalve form. In this way it should be possible to achieve a greater understanding of the evolution of cementation within the Bivalvia and to explain its origins.

There is a broader justification for studying the evolution of cementation in the bivalves. Other members of the Mollusca, brachiopods and even annelids also exploit

the cemented habit. It will be of interest to establish the extent of convergence in the mechanisms of cementation employed in the disparate groups.

1.3 NUTS AND BOLTS

Before reviewing the existing knowledge of cementation and outlining the principal objectives and approaches of this thesis, it is necessary first to set the scene. Morphological terms and a basic description of shell secretion in the Mollusca are needed.

1.3.1 Morphology and terminology

The bivalves comprise a class of the phylum Mollusca. They are characterised by an ancephalous visceral mass enclosed by two laterally compressed calcareous valves (right and left), united dorsally by a springy ligament. Figure 1.2 illustrates the basic morphological terms applicable to (a) dimyarian and (b) monomyarian bivalves.

The morphological terms utilized in this thesis conform broadly to those used in the *Treatise* Part N (Moore, 1969), and defined by Cox (p.N102-109) in that volume. Cox' definitions are not repeated here, but any terms which have either been introduced to the literature after the publication of the *Treatise* or have arisen as part of this study are defined and illustrated where they appear in the text. Basic parameters including valve height, width, length and umbonal angle follow the usage proposed by Cox in the *Treatise*.

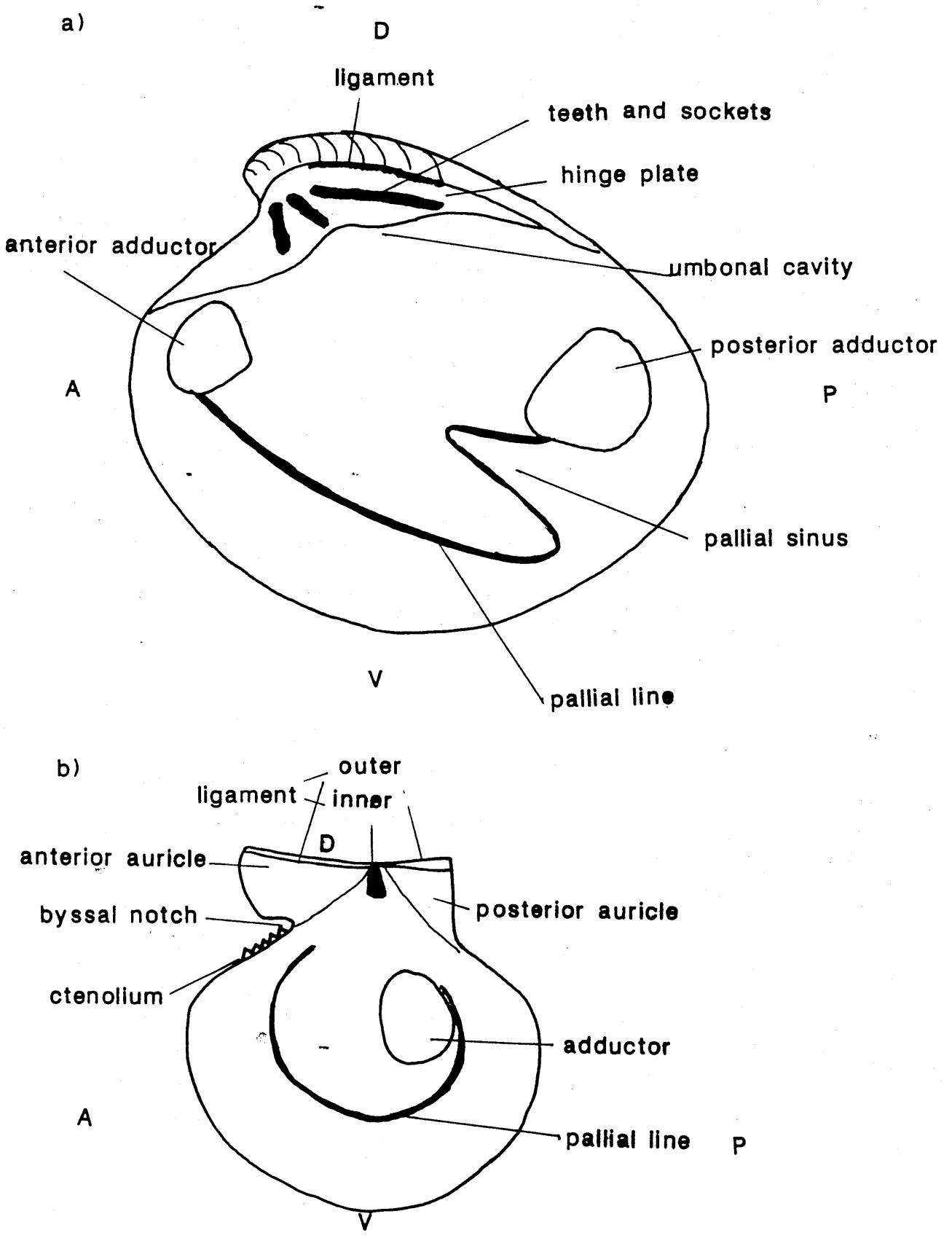


Figure 1.2: Morphological terms commonly used in this work, as applied to dimyarian and monomyarian bivalves. a) a generalised venerid and b) a generalised pectinid. A= anterior, P=posterior, D=dorsal and V= ventral.

1.3.2 The mechanism of bivalve shell secretion

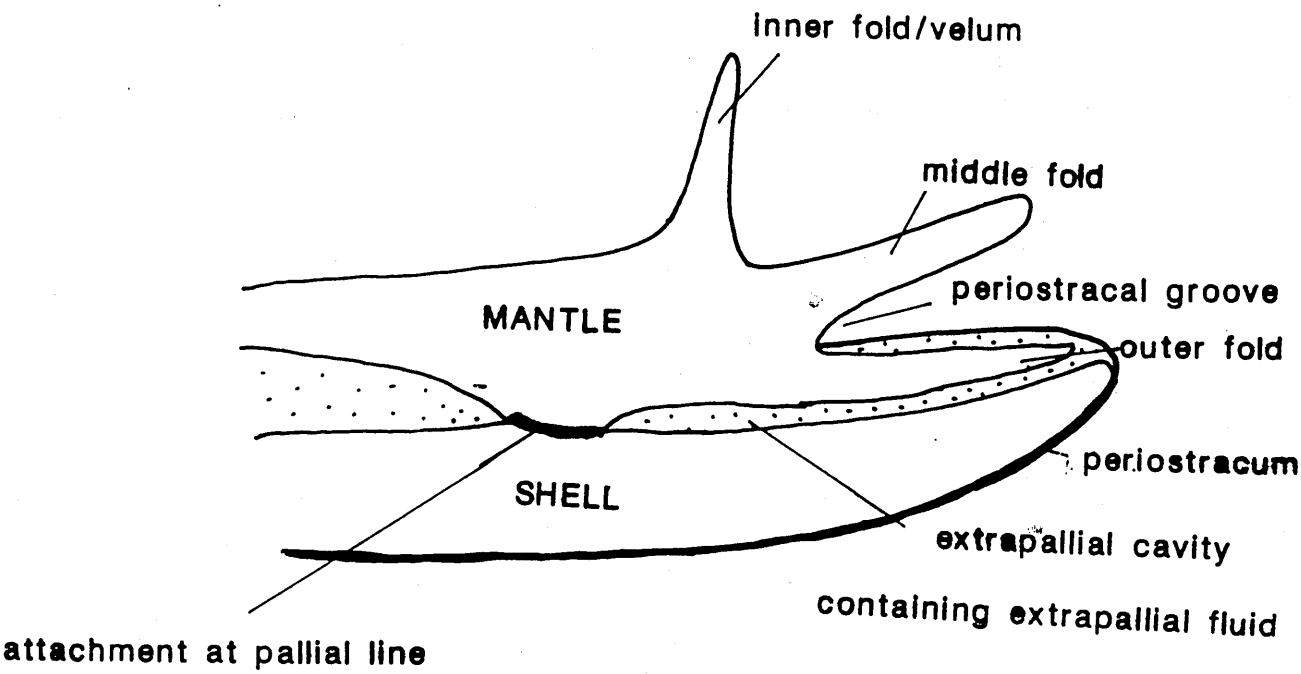


Figure 1.3: Cross section through the bivalve valve margin and soft parts to illustrate mode of shell secretion, based on Taylor, Kennedy and Hall (1969).

The mechanism of secretion of the bivalve shell is well understood. Since this process is intimately related to cementation it is appropriate that a brief account of shell secretion is given. Further reviews are supplied by Wilbur (1964), Taylor, Kennedy and Hall (1969a,b), Crenshaw (1980) and the references therein.

The body of the bivalve is shrouded in two mantle lobes which lie directly under the calcareous valves (see Figure 1.3). In most bivalves the edges of the mantle lobes are divided into three folds, although Waller (1978) has demonstrated that the primitive condition is twofold. The inner fold controls the water flow into the mantle cavity, whilst the middle fold bears the sensory organs. It is the outer fold that is actually responsible for the shell secretion.

The outside of the shell is covered in a thin tanned mucopolysaccharide layer, the periostracum, first identified by Gray (1833). This layer is continuous with the mantle and is secreted by the cells of the periostracal groove which lies between the outer and

middle mantle folds. The periostracum forms the template on to which the calcareous portion of the shell is laid down as calcite and/or aragonite within an organic matrix (Wilbur, 1964). The mantle tissue is separated from the periostracum and the already formed shell material by a thin fluid-filled cavity. The extrapallial fluid, secreted by the mantle tissues, has the composition of modified sea-water saturated with respect to calcium and carbonate ions, (Simkiss, 1965). It is from this fluid that the calcium carbonate shell material is nucleated, and as such, the extrapallial fluid plays the pivotal role in shell secretion. It is, as yet, unclear as to whether the fluid is basically sea water modified by the addition of mantle secretions, as suggested by Simkiss, or whether the mantle tissue is responsible for the entire secretion. Resolution of this debate hinges on finding a means of sampling this fluid without disturbing the animal inducing trauma and causing its secretory processes to change.

This mode of shell secretion, common to all Mollusca, is fundamentally different from that employed by the brachiopods, as discussed in Section 7.5.1.2.

1.4 PREVIOUS WORK

1.4.1 Oysters

Ostreiculture is of great economic importance in various parts of the world. It is therefore unsurprising that a certain amount of work has been invested on the study of oyster attachment. Yet this work has only addressed the initial attachment, for it is the success of this early ontogenetic stage which is of critical importance to the oyster farming industry. It is common practice to separate young oysters from their cultch (the substrate on which they have spatted) at an early stage (Yonge, 1960). Indeed the current procedure is that this separation be made after only 24 hours (S.Utting (MAFF), personal communication) or the spat are even prevented from attaching at all (J.Bayes (Seasalter Shellfisheries), personal communication). Consequently there has been no detailed work on cementation of postlarval oysters.

Early workers

Nelson (1924) and Prytherch (1934) studied the attachment of *Crassostrea virginica.* The former contended that the mantle was responsible for spreading the cement, whilst the latter cast the foot in that role. Prytherch's study included a detailed photographic survey of site selection by the pediveliger, and of the formation of a single byssus thread prior to the secretion of cement by the foot. Cole and Knight Jones (1939) followed similar procedures whilst studying the spatting of *Ostrea edulis*. Their study reveals a process closely similar to that described by Prytherch, with no evidence of mantle involvement.

Yet it is clear that the foot cannot be responsible for cementation throughout life, as the structure is lost within six days of settlement (Hickman and Gruffyd, 1971).

H. J. Cranfield

In the early seventies Cranfield published a series of papers on the earliest larval attachment of *Ostrea edulis* (1973a,b,c; 1974 and 1975) a result of a very detailed study of the first six hours after settlement. Cranfield's work showed that it was indeed the foot which effected initial cementation. Pedal glands deliver a tanned mucopolysaccharide similar in composition to byssal threads. He noted that during the secretion of the pedal cement the mantle folds were active but did not venture beyond the valve margins. However, after application of the pedal cement Cranfield observed the mantle secreting a cement. Histological examination of the mantle tissue revealed that gland cells in the inner fold contained a mucopolysaccharide similar in composition to that identified in the foot. Cranfield concluded, therefore, that the pediveliger made its cemented attachment by a mucopolysaccharide cement, originally supplied by the foot and usurped by the inner fold of the mantle. In doing so he reconciled the views of Nelson (1924) and Prytherch (1934) as separate parts of the same progressive developmental process.

C. Tomaszewski

Tomaszewski (1981) essentially repeated Cranfield's work using spat of *Crassostrea virginica,* but prolonged the survey until one week after settlement. His work

confirmed Cranfield's observations of initial attachment by pedal cement followed by mantle involvement. He went on to speculate that further attachment was probably periostracal but offered no evidence for this.

Carriker, Palmer and Prezant (1980), in their detailed study of the ultramorphology of the dissoconch of *Crassostrea virginica* chose not to investigate the actual contact between bivalve and substratum. There are no studies, known to me, which have examined attachment in more mature oysters.

1.4.2 Other taxa

Work on cementation in other taxa has been confined to speculation rather than experimentation and observation, e.g. Morton (1974), Nicol (1978) and Yonge (1979). Most workers have tended to prefer a scenario where attachment is effected by a fluid periostracal 'glue'. These claims will be dealt with in detail in Chapter 3.

1.4.3 The work of C.M. Yonge

".... few malacologists, now or tomorrow, will be able to work on any of these taxonomic groups without reference to him."

Morton (1986)

Yonge produced a multitude of papers on the biology of a vast number of bivalves. Many of these covered the cemented bivalves; indeed few of the living cementers escaped his attention. It was not the actual process of cementation that intrigued Sir Maurice, but more often the consequences of the habit on the organization of the mollusc. His survey of the cementing bivalves, however, culminated in a review paper (Yonge, 1979), in which he did speculate on the actual mechanism of attachment of the cemented rock scallop. Although Yonge never tackled the problems of evolution of the cemented habit nor studied palaeontological material, his work has been invaluable in this thesis. There is an inevitable tendency to pick up on his errors and speculations which do not conform to the present author's views, but that should not detract from the fact that his papers have considerably broadened our knowledge of

these taxa and have, indirectly, suggested the lines along which research should proceed.

1.5 THESIS AIMS

Clearly there is much to be learnt about the cementing bivalves. In order to be able to tackle specific problems about the multiple evolution of cementation within the class the answers to the following questions have been sought:

- How many clades have evolved the habit?
- How do modern bivalves cement and how many mechanisms exist?
- What are the preadaptive requirements which allow this mechanism to evolve?
- What constraints have prevented other bivalves from acquiring the cemented habit?
- What are the selection pressures which favour the acquisition of the cemented habit?

1.6 APPROACHES AND METHODOLOGY

The problem of the evolution of cementation in the bivalves concerns both palaeontology and biology. Approaches and techniques appropriate to both these disciplines have been adopted in this thesis.

Material

Where possible living material has been used for investigation. Native bivalves have been collected and observed at Dunstaffnage Marine Station, Oban, and Galway Bay, Eire. Additionally it has also been possible to maintain animals in seawater tanks at the Open University. Material was supplied by both the Ministry of Agriculture, Fisheries and Food and the University Suppliers from Millport, Isle of Cumbrae. In addition tropical taxa were obtained from Tropical Marine Supplies, Boreham Wood. Existing museum collections have been utilised to a large extent for both palaeontological and zoological material. Table 1.1 details these institutions and the abbreviations by which specimens are referred to in this thesis.

INSTITUTION	ABBREVIATION USED IN TEXT
Bristol City Museum	BCM
Cambridge University Department of Zoology	CZ
Mineralogisk Museum Copenhagen (Principally the unregistered Ivö Klack Collection)	DCM
Ministry of Agriculture, Fisheries and Food (Conwy)	MAFF
Muséum National D'Histoire Naturelle (Paris)	MNHN
The Natural History Museum (Palaeontology).	NHP
The Natural History Museum (Zoology)	NHZ
National Museum of Wales (Cardiff)	NMW
Oban-Dunstaffnage Marine Laboratories	OBAN
Oxford University Museum	OUM
Sedgwick Museum (Cambridge)	SD

Table 1.1: Institutions whose collections have been used in this study and the abbreviations used in this thesis.

With the occurrences of cementing bivalves so widespread it is unsurprising that several taxa are not readily obtainable in this country. For example, two families are restricted entirely to Australasian waters. In order to examine examples of all cementing bivalves I have relied on the good will of others in the donation of wet material for destructive research. Particularly important in this connection have been Professor B. Morton (University of Hong Kong), for the provision of *Dimya* and *Saccostrea*; Dr. W. Ponder (Australian Museum, Sydney), for *Cleidothaerus* and *Myochama*; Dr. P. Bouchet (MNHN), for *Etheria elliptica;* and Dr. N. Bourne (Canadian Department of Fisheries, Nanaimo), for *Hinnites giganteus.*

Palaeontological material, additional to that provided by museum collections, has been collected. The most extensive of these collections was made from the Middle Jurassic of Normandy, an area described in detail by Palmer (1974) and Palmer and Fürsich (1981). Supplementary material has been gathered from sites elsewhere in the Jurassic and Cretaceous of this country, as well as from the Upper Cretaceous of Denmark and

from my own pre-existing Plio/Pleistocene collections from East Anglia. Where applicable details of these localities will be given in the text.

All material referred to in this thesis is to be deposited in The Natural History Museum (London) in the collections of a suitable department, i.e. NHP or NHZ. Appendix 1 lists all the preparations for Scanning Electron Microscopy (SEM), giving their identifying number, method of preparation and locality of collection. All material used for scanning electron microscopy produced during this research has been deposited, whether or not referred to directly in this thesis. Owing to the perishable nature of the soft part preparations most preparations are at least duplicated, thus allowing the possibility of re-study.

Techniques

A wide range of techniques has been employed in this study, from standard palaeontological hard-part investigations, to preparations of soft tissue, X-ray microanalysis and behavioural studies. It has been decided that many of these techniques are too disparate to be placed in a single all embracing 'methods section'. Instead, methods have been described in the text at the appropriate point in the study. Although this may break the narrative at that point, this method allows the reader quickly to assimilate the reasons why a particular technique has been used in a particular instance. An exception to this is the use of electron microscopy which is described below.

1.6.1 Scanning Electron Microscopy (SEM)

Extensive use has been made of SEM. Work has been largely concentrated on the JEOL JSM-820 at The Open University, with supplementary observations made at The Natural History Museum using the much higher resolution of the Hitachi S 800. Stubs were mostly gold sputtered and examined in the microscope at accelerating voltages ranging from 8 to 15kV. Micrographs were taken on black and white negative film and processed in the standard way. Attention is drawn to the note in the preface of this thesis, page xvi.

Those micrographs reproduced in this thesis have scale bars as an integral part of the image, therefore no allowance needs to be made as to their enlargement. Many, however, also bear a numerical statement of the magnification which bears no resemblance to the final printed dimensions; this value should be ignored. Other information is also given on the micrographs, including working distance, in millimetres (WD) and accelerating voltage in kV.

1.7 THESIS LAYOUT

This thesis is divided into seven chapters. Chapter 2 identifies the individual occurrences of the evolution of cementation in the Bivalvia over geological time. This second chapter is rather dull but it does provide a data base of various anatomical and morphological features and other information, much of which will be referred to in later sections. The actual mechanism of cementation is examined in Chapter 3, whilst the fourth chapter notes the preadaptations required for this mechanism to evolve and assesses the chances of identifying these in the fossil record. Chapter 5 is a case study of a family, the Pectinidae, which appears particularly well preadapted for the cemented habit and charts its multiple evolution in the family. The question 'Why do bivalves cement?' is asked in Chapter 6, which explores the possible selective advantages of the acquisition of the habit.

Each of these chapters ends with a summary of the principal conclusions reached. Chapter 7, therefore, examines these conclusions in a very broad sense, both in relation to our understanding the evolution of the Bivalvia, including identifying the constraints which prevented certain taxa adopting cementation, and also for the evolution of cementation in other taxa and phenomena associated with the habit. Avenues for future research are also suggested.

CHAPTER 2
DRAMATIS PERSONAE

2.1 INTRODUCTION

Members of over sixteen families of bivalves have, or have had, the ability to cement to a hard substratum. In studying the evolution of cementation it is necessary to establish how many times the habit has appeared independently. Is there a single ancestral species that acquired the ability to cement, and then radiated to form the multitude of cementing bivalves, or have the preadaptations for that ability arisen and been exploited in several different clades?

2.2 PREVIOUS ATTEMPTS TO ASSESS THE NUMBER OF TIMES CEMENTATION HAS EVOLVED

Jackson (1890) sought to construct a phylogeny of the Bivalvia, in which he dealt with many of the cementing bivalves. He correctly stated that the irregular shell growth associated with cementation is of no value in determining phylogenetic relationships and in fact masks morphological features useful in comparison. However, he failed to recognise that the various cementing bivalves need not necessarily be closely related and may have arisen independently. He also lacked a palaeontological perspective, which led him to many erroneous conclusions. The grand phylogenetic lineage which Jackson constructed centred upon a descendant of *Pecten* acquiring the cemented habit to form the genus *Hinnites* which in turn evolved into *Spondylus* and finally into *Plicatula*. Today there is no evidence for this; not only does the fossil record show that these cementing genera appear in exactly the reverse order over geological time, but anatomical studies show all three to be clearly distinct. More recently Newell and Boyd (1970) have put forward the Pseudomonotidae, the only certain Palaeozoic cementing bivalves yet recognised, to be the ultimate ancestors of many of the Mesozoic cementers. This claim is more specifically dealt with in the

following sections, but may be rejected here simply on the grounds that the evidence they offered was slight, there being still some doubt that the pseudomonotids themselves are a distinct taxonomic unit, and because the claim was in part withdrawn by Newell in a personal communication published by Yonge (1979).

Nicol (1978), Yonge (1979), and Vermeij (1987) have all published lists of families of cementing bivalves attempting to show the number of times that the habit has evolved independently. None is exhaustive and none contemplates the possibility of cementation arising in taxonomic units below the family level. For example, Yonge suggests indirectly that the habit evolved at least ten times, but fails to cite many of the fossil groups or to recognise the multiple acquisition of the habit within the Pectinidae.

The division of the cemented bivalves into distinct clades in which the habit was independently acquired is problematic. Convergent features such as gross shell distortion, loss or reduction of the foot and loss or reduction of the anterior adductor may be misconstrued as synapomorphic features uniting two groups - thus producing a polyphyletic taxon. There is also a resistance to regarding cementing bivalves as anything other than oysters. Fürsich and Palmer (1982) believe this to explain in part the somewhat late recognition of *Eonomia:* this may also explain the similar ignorance of *'Eopecten'* (see section 5.2.4).

2.3 NEW PROPOSED SCHEME

Below I have detailed my own account of the clades within the Bivalvia which have independently evolved the cemented habit. This is the result of the examination of both fossil and living material and anatomical studies of living molluscs, supplemented by extensive literature searching. Unless otherwise stated all observations are my own.

2.3.1 AIMS

I have attempted to identify each individual clade of cementing bivalves, both living and fossil, giving information on each which should be sufficient to distinguish it from the others. This work is NOT an attempt to revise the taxonomy of the cementing bivalves - the spread of families and genera concerned makes such a revision unfeasible within the scope of this project. The classification used by Newell (1969) in the *Treatise* is followed except where recent literature justifies its modification, for example in the case of the pteriomorphs reclassified by Waller (1978).

2.3.2 INFORMATION GIVEN

The information given for each clade falls under the following headings.

Valve of attachment: An indication is given as to whether attachment is by the right or left valve, or whether there is no particular preference. The ontogenetic stage at which cementation occurs in the living bivalve is given (Chapter 4 gives information on the timing of settling in fossil cementers). Where relevant the extent of attachment is dealt with. However this feature is determined by at least two processes;

(i) the genetic predisposition of the bivalve, and

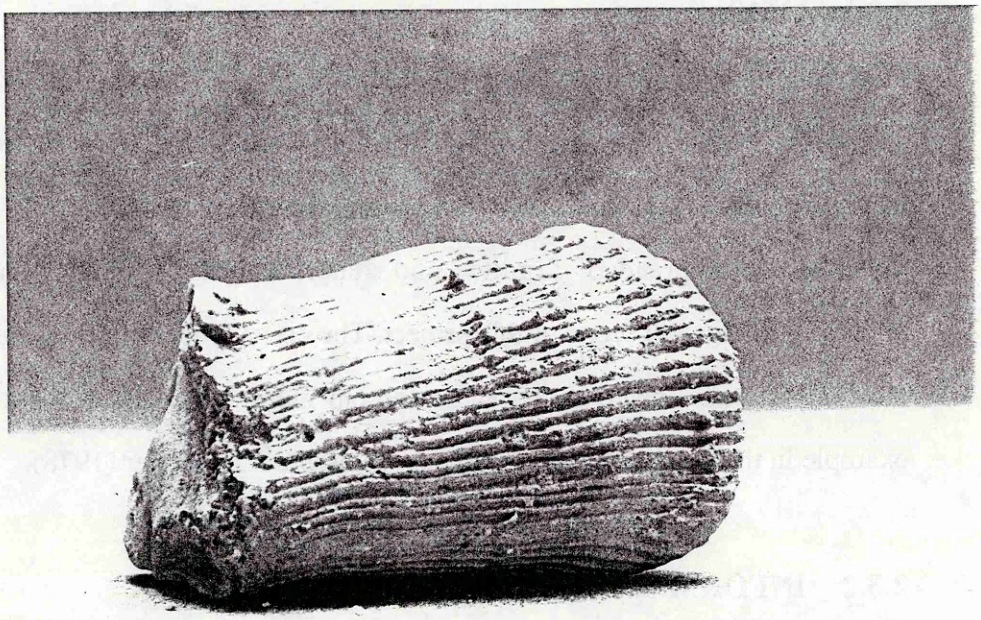
(ii) the effect of the size of substratum.

Given (ii) the extent of attachment may vary within a given species according to the substratum. Figure 2.1 shows the Campanian *Spondylus labiatus* from Ivö Klack in Sweden with two differently sized substrata, illustrating the differing extent of attachment and the effect that this has on valve morphology.

Adductor musculature: Dimyarian or monomyarian.

Anatomical features: Other features of the soft part morphology are noted where they are distinct for a clade or where their presence is judged to be important in the cementation process or a consequence of the habit. For example, the presence or absence of the foot is given.

a)



b)

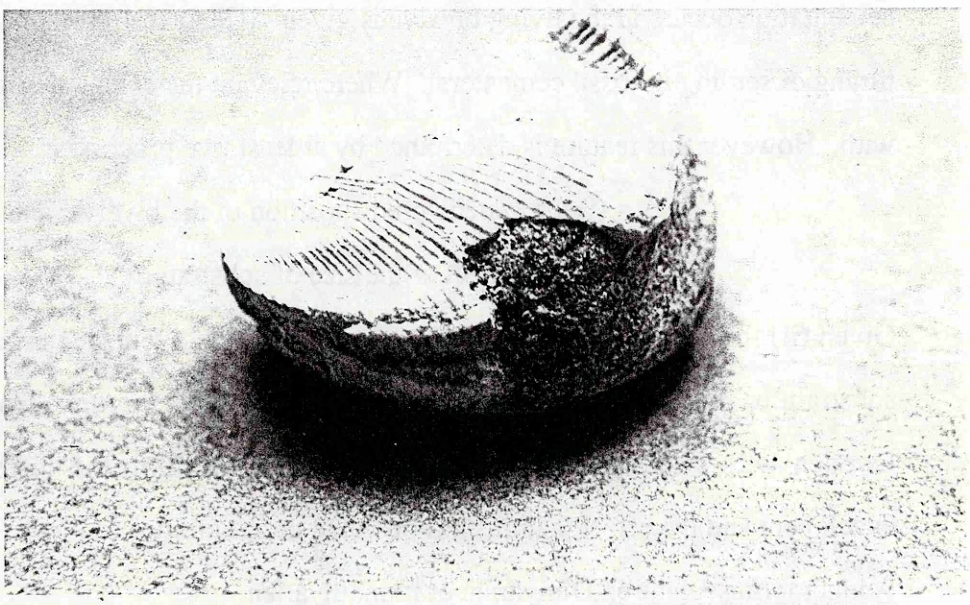


Figure 2.1: Varying extent of attachment and its effect on gross morphology in Campanian *Spondylus labiatus* from Ivö Klack. Material held in DCM, unregistered. a) Individual with small scar (substratum lost), width=31mm. (b) Individual attached for almost entire extent of valve to a gneiss pebble, height=48mm. Rephotographed from original contacts.

Shell morphology: Gross shell morphology is described.

Shell mineralogy: All bivalves contain aragonite in the pallial and adductor myostraca. Aragonite may also be in the main part of the valve, either entirely (the primitive bivalve condition, Taylor, 1973) or in part. In the latter case the rest of the valve is composed of calcite. Shell microstructure is recorded in Appendix 2.

Ecology and geography: The biogeographic and palaeobiogeographic range of the clade is given along with information about the habitat in which the animals live.

Taxonomic diversity: An attempt is made to assess the taxonomic diversity displayed.

Geological Range: First and last appearances in the fossil record are given. Unless otherwise stated this information is derived from Sepkoski (1982).

Discussion: This section justifies the assignment of the group to a clade, explaining the grounds on which it may be separated from other cementing bivalves.

The bulk of the information given for each clade is summarised in Table 2.1, located at the end of section 2.3.3 for ease of direct comparison.

2.3.3 THE NEW SCHEME

2.3.3.1

Subclass AUTOBRANCHIA

Superorder PTERIOMORPHIA

Order OSTREOIDA

Superfamily AVICULOPECTINACEA?

FAMILY **PSEUDOMONOTIDAE** Newell, 1938

Material from this group of cementing bivalves is scarce. Material of the Visean *Pachypteria* sp. collected by D.J.C. Mundy at Stebden Knoll, Yorkshire is held at the NHP for description by N.J.Morris. This material was generously shown to me for

study for the compilation of this section,and in no way preempts the forthcoming description by Morris. All observations here are based upon my study of *Pachypteria* backed up by the work of Newell and Boyd (1970) on two other cementing pseudomonotid genera, *Prospondylus* and *Pergmavalvula.*

Valve of attachment: Cementing pseudomonotids invariably attached by the right valve. *Pachypteria* was observed to have cemented late in ontogeny (height - 8mm), after a clearly byssate stage. Newell and Boyd (1970) note that *Prospondylus liebeanus* attached after 20mm and *Pergmavalvula* at 2-4mm.

Adductor musculature: Single muscle scar (posterior??), centrally placed.

Anatomical detail: Little available evidence. The pallial line, dorsally placed away from the ventral valve margins, is clearly disjunct in *Pachypteria.*

Valve morphology: Moderately inequivalve and inequilateral, the left valve more convex than the right. The juvenile shell is 'pectiniform' with ribbing and a byssal notch - no ctenolium observed. In the attached stage the byssal notch is occluded and the right valve becomes distorted. No xenomorphism observed. Edentulous. Ventral migration of the hinge line of the attached valve.

Valve mineralogy: Newell and Boyd (1970) state that the pseudomonotids have a bimineralic shell with outer calcitic and inner aragonitic layers.

Ecology: The pseudomonotids are associated with shallow shelf reefs. Brunton and Mundy (1988) describe the setting of *Pachypteria* sp. discovered at Stebden Knoll. They describe the bivalve as dominating the epifauna of an algal reef in very shallow water. This large collection of *Pachypteria* shows that locally this bivalve was far from rare, although previously the genus has only been known from five specimens collected in Belgium by de Koninck in the last century.

Geological range: The cementing pseudomonotids so far discovered have a disparate fossil record, with *Pachypteria* found only in the Lower Carboniferous Visean stage and the genera *Prospondylus* and *Pergmavalvula* with a limited range, Leonardian to Guadalupian, in the Upper Permian, (Newell and Boyd, 1970).

Taxonomic diversity: Low.

Discussion: Contrary to the view of Newell (1938) and Nicol (1944) species of the genus *Pseudomonotis* do not cement, although inspection of material of this genus at the NHP shows that the lower right valve is frequently distorted. Hence the cemented habit in the family Pseudomonotidae has evolved below the familial level in particular genera within the family. In their monograph Newell and Boyd (1970, page 251) speculate that the cementing habit may have evolved iteratively in the Pseudomonotidae. However the low abundance of material and paucity of general information makes such an assertion difficult to support. Without a clear idea as to the life habits of Late Carboniferous pseudomonotids, to close the stratigraphic gap, it would seem more parsimonious for the present to regard these genera as a single clade.

The taxonomic distinctiveness of the family Pseudomonotidae is questionable (N.J.Morris, personal communication). It seems most likely that the family is closely related to and probably derived from the Aviculopectinidae. The aviculopectinids are a family of bysally attached pectiniform bivalves, pleurothetic on the right valve, ranging from the Upper Devonian to the Upper Jurassic. Evidence from those listed in the *Treatise* suggests that some genera eg. *Philippiella*, lost their byssal attachment during ontogeny to become free lying. It is easy to envisage a scenario by which some of these individuals which lost byssal attachment became cemented. Within the Pectinidae we see a similar pattern of loss of byssal attachment leading to free living forms such as *Chlamys opercularis* and cemented forms eg. *Chlamys pusio*.

Grand claims have been made for the pseudomonotids as ancestors of the oysters (Newell and Boyd 1970 and 1989). Principle objections lie in the oysters cementing exclusively by the left rather than the right valve, and differences in shell structure.

2.3.3.2 Superfamily PECTINACEA

FAMILY **PECTINIDAE** Rafinesque, 1851

I have identified four separate occurrences of the cemented habit arising in the Pectinidae. This multiple acquisition is discussed in detail as Chapter 5. Here it is sufficient only to name these four clades and give a generalised account of the family as a whole. Although clearly distinct, each cementing pectinid clade shares several major features, which do not require repetition.

The separate clades are as follows;

1] '*Eopecten*' described as cementing in Section 5.2.4 collected from the Bathonian of Normandy.

2] *Prohinnites* Cretaceous (Valanginian - Aptian), see Section 5.2.2.

3] *Hinnites* Miocene - Recent, see Section 5.2.1.

4] *Chlamys pusio* Recent , see Section 5.2.3.

Valve of attachment: All attach by the right valve, to varying extents and at a varying stage in the life history.

Adductor musculature: Monomyarian, retained posterior adductor.

Anatomical detail: Dissections of living *Chlamys pusio* and *Hinnites giganteus* show that both have a large and very active foot. The mantle lobes are highly mobile, the middle one of which has well developed sensory tentacles and pallial eyes.

Valve morphology: Highly inequivalve and, ignoring the asymmetry produced by the auricles, equilateral. *Chlamys pusio, Prohinnites* and *Hinnites* have deeply convex right valves, whereas in '*Eopecten*' the right valve is virtually flat. Idiomorphic valve growth produces radial pectinid ribbing, which is lost on cementation. The right valve of individuals prior to cementation shows a deep byssal notch with a ctenolium. Onset of cementation occludes the byssal notch. Edentulous. Amphidetic ligament within triangular pit.

Valve mineralogy: Calcitic outer layers and aragonitic inner layers.

Ecology and Geography: Discussed in Chapter 5.

Taxonomic diversity: The sporadic occurrences of cementation within the Pectinidae are not marked by any great proliferation of taxa. The lineages sparked off appear to consist of no more than a single genus or species each.

Discussion: There is a general tendency to refer to any cemented pectinid as *Hinnites* (Bernard, 1986). As Bernard points out this is clearly an error. Material in Chapter 5 will show that the cited cases are unrelated instances of the habit evolving from a highly preadapted group.

2.3.3.3 FAMILY **SPONDYLIDAE** Gray, 1826

Valve of attachment: All spondylids are invariably pleurothetic on the right valve. All specimens examined show some signs of cementation to widely varying extents. This attachment is effected either by the valve itself or by flangous outgrowths, see Figure 4.12. There is evidence that having lifted off from the substratum the growing edge of the shell is able to resume cementing should a suitable hard surface be encountered; e.g. *Spondylus aurantius* NHZ 40.1 19.39.

Secondary freedom has been acquired in the Cretaceous *S. spinosus* and the Recent *S. imperialis*.

Adductor musculature: Monomyarian. Large posterior adductor muscle situated towards the centre of the valves. Dissection of *S. gaederopus* reveals a high proportion of quick muscle.

Anatomical details: Specimens of living *S.gaederopus* and preserved *S.histryx* have been dissected in this study; both reveal that only a small foot is present. Dakin (1928) noted that the foot of *Spondylus* lacks retractor muscles. Both these observations imply that the foot in the adult is of only restricted use, probably acting

in a cleansing role. Observations of the living specimens in the aquarium showed that the mantle margins were highly mobile; capable of both deep retraction and extension. The middle mantle lobe is very well equipped with sensory tentacles and pallial eyes. Dakin (1928) showed that the anatomy of the animal bears a marked resemblance to that of *Pecten*, except for differences in the velum and nervous system.

Valve morphology: Adult spondylids are in general highly inequivalve and equilateral attaining large sizes (some modern examples exceed a shell height of 150mm). The right valve is more convex and taller than the flatter left. Slightly auriculate, no byssal notch in the adult. Marked ventral migration of the hinge line on the attached valve, producing a triangular shaped area above the long amphidetic hinge line. Alivincular resilium sunk into a deep triangular pit at the centre of the hinge. In each valve the ligament pit is flanked by two large isodont teeth and the corresponding sockets. The pallial line is entire. Valve margins may be either plain or crenulate. Shell ornament varies considerably, displaying radial ribs, long solid spines and commarginal flanges. The latter two ornaments are more conspicuous on the right valve, and there would appear to be a trend for increasing spinosity over evolutionary time (see Section 4.4.3) However, the Recent *S. pacificus* is devoid of any spines or flanges. Although the left valve may be distorted by the underlying substrate, I have observed no xenomorphism.

In those species that have become secondarily free the valves are more equivalve and there is little or no development of the cardinal area. There is also a marked lack of flanges although spines on the right valve are often well developed.

Prior to any attachment the young spondylids have a pectiniform appearance with a byssal notch, lacking a ctenolium, see Figure 4.1(c).

Valve mineralogy: Thin outer calcitic and thick inner aragonitic shell layers. The aragonite extends far outside the pallial line.

Ecology: Yonge (1973) and Logan (1974) describe *Spondylus* as a solitary bivalve common on tropical reefs at depths up to 20 metres. A single specimen of *S. gussoni* in the Sedgwick Museum (D20920) was dredged from 1120 metres. Logan stresses that the principal habitat of *S. americanus* is as a crevice dweller. Taylor (1971) notes that the genus is common on coralline substrates and does not colonise rock substrates (which the oysters and *Chama* do). In the fossil record, however, Surlyk and Christensen (1974) describe a massive encrustation of intertidal *S. labiatus* from the Early Campanian at Ivö Klack in Sweden on gneiss boulders. Their distribution shows them to be characteristic of the highest epifaunal zone. Examination of this material in June 1989 revealed that many individuals were clustered together in 'colonies', Figure 2.2 .

Jurassic *S. consobrinus* collected off the Bathonian sponge reef at St. Aubin - sur - mer in Normandy were solitary but of patchy distribution over the reef as a whole. Palmer and Fürsich (1981) maintain that the species is found only on the sheltered undersides of sponge fronds, however specimens were collected from the upper surfaces, although these may have been shadowed by higher fronds. I have also collected specimens of *Spondylus* from the Lower Gault (Albian) at Munday's Hill, near Leighton Buzzard. These specimens are attached to small phosphatic nodules and would not have been able to select sheltered attachment sites.

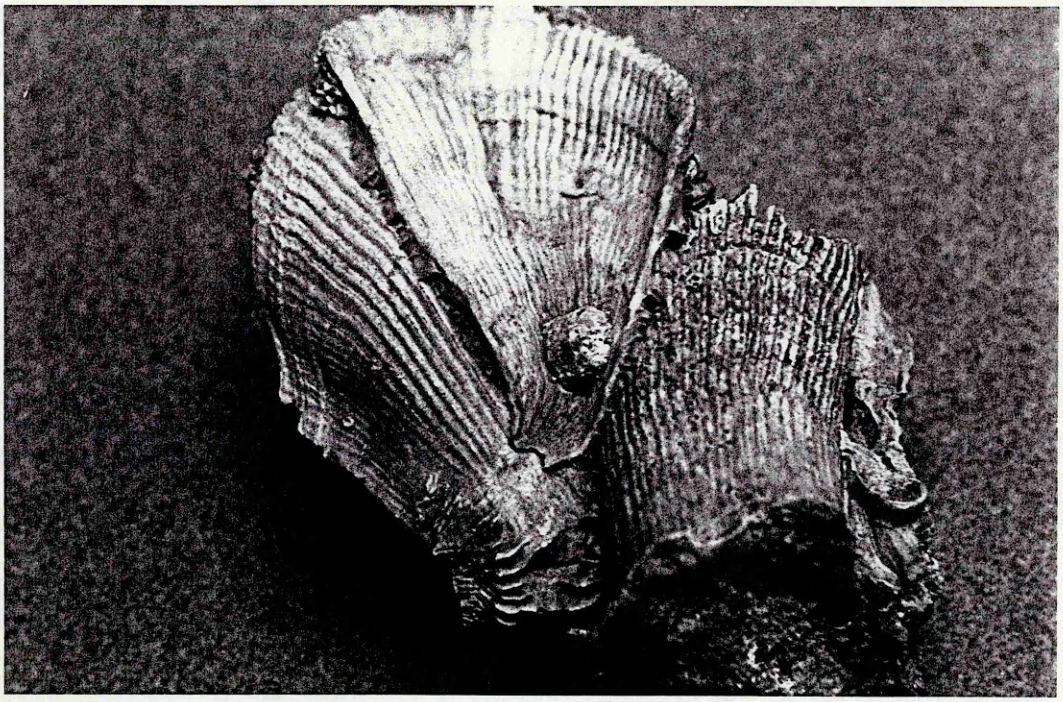


Figure 2.2: Gregarious settlement of Campanian *Spondylus labiatus*. From Ivö Klack collection held, unregistered, in DCM. Width of centre individual= 31mm. Rephotographed from contacts of originals.

Taxonomic diversity: The Spondylidae is a monogeneric family, split into three subgenera; *Spondylus, Eltopera* and *Corallospondylus*. There are, however, many species described. This may in part be due to over zealous splitting of a genus with a highly plastic morphology and a high commercial value. Zavarei (1973) enumerates 42 species from the Upper Cretaceous, 83 Tertiary and Quarternary and 63 living species. An impressive array of the living species are illustrated by Lamprell (1987).

Geological range: Jurassic (Bajocian) to Recent, emended here.

The *Treatise* gives a lower limit for the Spondylidae as the Jurassic but gives no indication of stage. Jurassic spondylids are rare in collections and descriptions,and some, for example those held in the Sedgwick Museum Museum (F21710), are more

likely to be plicatulids. However, I have collected *Spondylus consobrinus (sp.?)* (NOR/005) from the type Bajocian section at St. Hônorine, Normandy.

Discussion: The Spondylidae are unquestionably members of the Pectinacea. There is close agreement between their anatomy (Dakin 1928), their shell structures and the juvenile forms. The only other recognised cementing members of the Pectinacea are within the family Pectinidae (2.3.3.2): the spondylids are clearly distinct from these, lacking a ctenolium, having a greater distribution of aragonite in the shell and lacking tentacles on the velum (Waller 1978). Although Jackson (1890) believed that *Spondylus* was derived from *Hinnites*, there is no evidence for this, as *Hinnites (*first appearing in the Miocene) is a very much younger genus. Moreover, Waller (1978) shows that the *Hinnites* is the more derived form.

Various authors have considered the possibility of a close relationship with the Plicatulidae eg. Yonge (1973), Jackson (1890) and Cox and Hertlein (in Moore, 1969). Such a close relationship is founded on plesiomorphic convergent features such as the monomyarian condition, and the possession of large hinge teeth. Yonge (1973) and Waller (1978) show conclusively that the Plicatulidae belong not to the Pectinacea but to the Plicatulacea, and that the two superfamilies have been distinct since at least the Middle Triassic.

2.3.3.4 Superfamily BUCHIACEA

FAMILY **TERQUEMIIDAE** Cox, 1964

Material belonging to this family is scarce.

Valve of attachment: The *Treatise* suggests that this family cement exclusively by the right valve. Whereas Cox (1964) claims that the genus *Enantiostreon* cements by either valve, Seilacher (1954) believes that left valve cementing *Enantiostreon* are true

oysters. Examination of the small collection of specimens at the NHP does nothing to resolve this. Specimen NHP 1208 labelled *Enantiostreon spondyloides* is clearly not an ostreid. The specimen is cemented by the left valve, contrary to what is stated by the note accompanying it. From the small amount of material available it is not possible to state whether this specimen is truly a terquemiid or perhaps a member of another clade.

The presence of a byssal notch in the most juvenile shell suggests early byssate attachment.

Adductor musculature: Study of internal mould at the NHP 1578 indicate that the genus *Enantiostreon*, at least, is monomyarian.

Anatomical detail: Unknown.

Valve morphology: Inequivalve and inequilateral. Right valve more convex. Highly distorted after attachment, but with strongly ribbed ornament. Ventrally migrated hinge line on the right valve with a broad cardinal area, edentulous. Median ligament extends through the area.

Valve mineralogy: Outer calcitic layers. Specimen NHP 1578 lacks internal shell detail and thus presumably had an aragonitic shell layer lost during diagenesis.

Ecology and geography: Little information.

Taxonomic diversity: The taxonomic diversity is difficult to assess, since a number of enigmatic genera, such as *Placunopsis* were placed by Cox (1964) into this family, apparently without justification.

Geological range: (?Permian) Early Triassic to Upper Jurassic (Oxfordian). Newell and Boyd (1970) claim members of this family from the Permian but it is uncertain how these relate to pseudomonotids.

Discussion: Cox (1964) erected the family during preparation of the *Treatise*. Here he considered the family to belong to the superfamily Pectinacea, yet considered it possible that the terquemiids were ancestors of the oysters. Indeed *Terquemia* and *Enantiostreon* do closely resemble the oyster genus *Lopha*, but for their attachment by

the right rather than the left valve. However, the Terquemiidae cannot be considered as merely right valve cementing oysters as they lack the characteristic derived ostreid microstructure and mineralogy. As with all putative ancestors of the oysters, which are pleurothetic on the right valve, inversion after the cemented habit has evolved is rather difficult to envisage. In the absence of proven examples of inversion of the Terquemiidae, a link with the Ostreidae rather than convergence, must be treated with some scepticism.

Stenzel (1971) notes that there are no oysters that cement by the right valve. This assertion will be discussed in detail in Section 2.3.3.8. Although I accept that the Terquemiidae are a distinct clade of cementing bivalve, separate from the true oysters, it may be that the family has also acted as a dustbin for right valve attached oyster species that do not fit the conventional view of oysters.

The amount of material available to me for this study is insufficient for me to make my own judgement on the validity of this group as a distinct clade, and hence I must defer to the work of Cox (1964).

2.3.3.5 SUPERFAMILY **DIMYACEA** Fischer, 1886

Valve of attachment: Invariably attach by the right valve.

Adductor musculature: Heteromyarian, virtually trimyarian as the larger posterior adductor muscle has two distinct attachment pads for the quick and catch muscles.

Anatomical detail: No foot. Highly extensible mantle margins with sensory tentacles well developed on the middle lobe. *Dimya* has a vestigial heart, made redundant, Yonge (1978b) states, owing to the small size of the mollusc coupled with its immobility.

Valve morphology: Small equilateral circular valves. Inequivalve, the right being in general flatter and larger than the convex left valve. Both valves are thin with a shiny

appearance, covered in minute concentric frills. Resilium, and two cardinal crurae. Pallial line dorsally inset and frequently disjunct. Alivincular ligament.

Valve mineralogy: Calcitic outer and aragonitic inner shell layers.

Ecology and Geography: The modern distribution is in deep waters in the lower latitudes. Their scarcity in more shallow shelf seas has led to a general ignorance of the superfamily as a whole.

Taxonomic diversity: Today there are at least four genera of dimyids recognised, many species of which are only just being reported.

Geological range: Upper Triassic (Carnian) to Recent. (Revised for this study - see below.)

Discussion: Cox and Hertlein in Moore (1969) place the family Dimyidae within the superfamily Pectinacea. Although identical to the Pectinidae and Spondylidae in valve microstructure and mineralogy, the family is clearly distinct from all other members of the Pectinacea in being di- rather than monomyarian, and as such ought to be removed from that superfamily.

Yonge (1975) removes the Dimyidae, along with the Plicatulidae, and elevates them to the superfamily Plicatulacea. He believed that the monomyarian Plicatulidae were evolved from the dimyids. Waller (1978) provided the evidence that this was unlikely to be true (see 2.3.3.6). Waller gave the Dimyidae their own superfamily, the Dimyacea, retaining it with the Plicatulacea and the Ostreacea to form the order Ostreoida. The derived character state he uses to distinguish the ostreoids from the Pectinacea is the lack of a foot. However, this is, I feel, an inadequate synapomorphy to utilise: the loss or reduction of the foot is seen as a convergent feature in most of the cementing bivalves.

The correct taxonomic position of the Dimyacea might be resolved by examination of the juvenile shell, prior to attachment.

The inclusion of the genus *Atreta* Étallon within the family Dimyidae.

Atreta Étallon (Upper Triassic to the Upper Cretaceous) has long been regarded as an enigmatic genus of cementing bivalve. Diagenetic loss of the inner shell layers has deprived us of information about the musculature, which would be invaluable in ascertaining the taxonomic position of the genus.

Atreta is far from uncommon. On the Bathonian sponge reef at St. Aubin - sur - Mer in Normandy, *Atreta retifera* is the dominant encruster of the fronds of the calcisponge *Platychonia,* frequently occurring in layers of successive spat falls. In the Cenomanian to Maastrichtian *Atreta nilssoni* is a common encruster on the tests of *Echinocorys*, (Hammond, 1988).

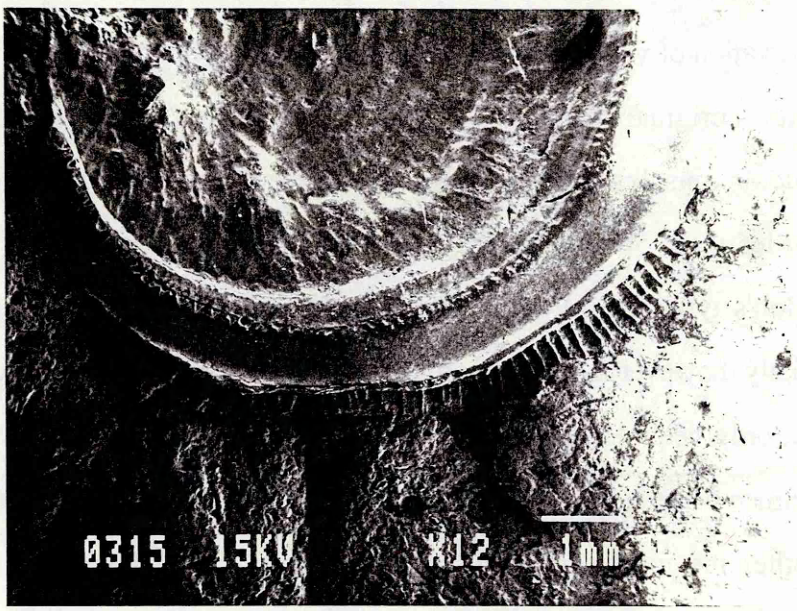


Figure 2.3: Right valve of *Atreta* attached to phosphatic nodule, collected from the Lower Gault at Munday's Hill, near Leighton Buzzard. Stub EMH0315.

Description: Inequivalve, virtually equilateral circular shaped valves , attached to hard substrata by the right valve. The left valve, less commonly found, is weakly

convex with a concentric flanged ornament. The right valve has a bowl shaped portion with an apron on the ventral margins that curves asymptotically to the substratum. The edge of this apron is frequently ribbed, see figure 2.3.

Diagenetic aragonite dissolution of the inner shell layers in the vast majority of specimens has led to details of adductor musculature and pallial attachment being obscure. The internal face of the outer shell layer, revealed by dissolution, is characterised by radial anastomosing ridges, see figure 2.3. A circular region of the umbo of the right valve, 1-1.5 mm in diameter, is frequently missing in specimens; attributable, I believe, to a non attached juvenile portion of the shell.

The external appearance of *Atreta* is very similar to that of the Dimyidae and certain plicatulids - hence the possibility that it may be related to either family. Distinction between the two families is largely based on the adductor musculature, the lack of preservation of which in *Atreta* has impeded its assignment to a family.

Étallon's original description in 1862 states that the specimens he observed had two adductor muscles, which would imply a dimyid affinity. However Cox (1964) regarded these observations as "doubtful", "without justification" and "imaginative". Étallon's types are missing, and therefore his assertions cannot be checked. It is unlikely, however that he had any particular preconceptions as the dimyids had, at that time, only been described as fossil forms from the Tertiary. Cox never identified a specimen of *Atreta* with preserved inner shell layers and was thus unable to determine whether the mollusc was di- or monomyarian. Although he acknowledged the resemblance to *Dimya,* Cox chose to place the genus within the Plicatulidae in the *Treatise*. This is, in my opinion, totally unjustifiable.

Vokes in 1979 wrote of the similarity between *Atreta* and *Dimya* but claimed that the former had only a single muscle scar. It is not clear whether this was his own obsevation or whether it was information borrowed from Cox.

More recently Hodges (1987) attempted to show that the genus *Atreta* is a member of the Dimyidae, claiming to have discovered a specimen of the left valve of *Atreta*

intusstriata of Liassic age, bearing two adductor scars. Study of the specimen held in the National Museum of Wales (NMW 22G . 174) reveals no evidence for two muscle scars, nor even any that the valve is truly of *Atreta*. Clearly, if adductor musculature is to be used to determine the taxonomic position of this enigmatic genus, then a specimen of the fixed valve should be used.

In the course of this study a re-evaluation of the taxonomic position of *Atreta* has been made, suggesting that it indeed belongs to the family Dimyidae. The evidence is fivefold, based on gross morphology, adductor musculature, presence of crurae micromorphology and shell microstructure.

-Gross morphology

All modern Dimyidae have small roughly circular valves, whereas Plicatulidae have a more scapuloid outline, the dorsal portion being flattened. No specimens of living and fossil plicatulids examined in the collections of the Natural History Museum were observed to have a circular outline. Clearly the valves of *Atreta* thus bear a closer resemblance to the Dimyidae than to the Plicatulidae. It would seem that all family descriptions of the Plicatulidae that include the term 'circular valves' have been modified to accommodate *Atreta.*

-Adductor musculature

Mindful of the value of discovering individuals of *Atreta* with preserved inner shell layers a specific search was made for such specimens. Despite the abundance of this genus on the Bathonian sponge reef at St. Aubin none is preserved with inner shell layers. This is not unduly surprising given the very rapid diagenetic loss of aragonite which has been reported for other localities in this region, see Section 5.2.4.

Collections of *Atreta nilssoni (?)* were made from a nodule bed in the Lower Gault (*Hoplites dentatus* zone - J. Eyers personal communication) at Mundays Hill, Heath and Reach (near Leighton Buzzard) in Bedfordshire (N= >400). The locality also yielded fragments of ammonite preserved with aragonite, indicating the possibility that the inner shell layers of *Atreta* may be intact. One specimen appears to show two

'platforms' in the posterior and anterior parts of the valve which might be interpreted as muscle scars. This specimen has been mounted for electron microscopy on stub EMH0317. Collection from the top of the Lower Gault at Burwell Pit (Cambridgeshire) has yielded a dimyarian left valve (Bu8/90), which I believe to be *Atreta*. However, as previously noted with reference to Hodge's (1987) claim, disarticulated left valves are not a sound basis for assigning the taxonomic position of an enigmatic cemented bivalve, known principally from its attached valve. Nevertheless, there are better grounds for accepting this individual as an *Atreta* than Hodge's specimen. The specimen is free from the matrix, thus revealing its entire morphology. It was also collected from a phosphate nodule band in which the only bivalves of comparable size are the attached valves of *Atreta* and *Pycnodonte*. Bu8/90 can be excluded from the latter genus as it is di- rather than monomyarian.

-Presence of crura

Specimen (VN/6) was collected from the Oxfordian at the Falaise des Vaches Noires, near Houlgate, Normandy. Although preservation of aragonite shell layers is not characteristic of this deposit this specimen of a gryphaeid oyster is encrusted by several plicatulids and a single *Atreta* in which the inner shell layers are clearly discernible. This preservation of the aragonitic portion of the shell has revealed details of the hinge line of the *Atreta*. A small ligament pit is flanked by small divergent crura, a condition paralleled in modern dimyids.

-Micromorphology

The anastomosing riblets on the inner face of the outer shell layers are characteristic of *Atreta*. Identical riblets can be observed through the thin inner shell layers of Tertiary *Dimyodon deshayesiana* NHP specimen 69922. Also Bayer (1971, his Figure 71) shows a similar ornament in the modern *Dimya tigrina*. I have observed no plicatulid with this ornament.

-Shell structure

Detailed shell microstructures have been determined in Apendix 2. *Plicatula* has a calcitic foliated outer shell layer with a thin outer prismatic layer, whereas the foliated calcite outer shell layer of *Dimya* lacks outer prisms. Determinations of the shell microstructure of *Atreta* show that, as with *Dimya,* there is no outer prismatic layer.

During the preparation of this thesis Professor Fürsich has brought to my attention the forthcoming paper by Fürsich and Werner (in press) which also describes a dimyarian specimen of *Atreta* with radiating riblets, thus confirming my assertion that the genus belongs to the family Dimyidae.

The inclusion of the genus within the family Dimyidae has two important implications:

-the geological range of the family is extended back into the Carnian (Upper Triassic), rather than the Bathonian (Middle Jurassic) as stated by Sepkoski (1982).

- a shift in niche over evolutionary time is indicated. Modern dimyids are found in deep water, of several hundred metres, on the edge of the continental slope (Vokes 1979). However, *Atreta* is abundant in shallow water deposits, such as the Bathonian sponge reef community described by Palmer and Fürsich (1981).

2.3.3.6 SUPERFAMILY **PLICATULACEA** Watson, 1930

Valve of attachment: Exclusively by the right. Cementation commences at an early stage of life history and continues for a variable time.

Adductor musculature: Monomyarian. The posterior adductor occupies a central position in the valve.

Anatomical detail: Dissection of a preserved specimen of *Plicatula imbricata*, loaned by J. Taylor, showed that the adult possessed no foot. However, Watson (1930)

states that it is "practically absent" and mentions having found a small grooved ridge which may represent the vestigial foot, although it contains no muscles or byssal gland. The middle and inner mantle lobes are poorly developed, the former possessing only small tentacles and no pallial eyes.

Watson (1930) notes that the gills are highly simplified.

Valve morphology: Subequilateral and inequivalve, the attached right valve being more convex. The ostreiform, subtrigonal valves are highly distorted and irregular, and may show a crude xenomorphism. The cardinal area is small, with two large isodont teeth and the corresponding sockets in each valve. A deeply sunk resilium lies between the two teeth. Integripalliate. The commissure is often notably zigzag, not unlike *Arctostrea*. The majority of species have an ornament of strong radial ribs, which produce the shape of the commissure, but some, for example *P. fistulosa*, bear spatulate spines which in some instances effect cementation.

Valve mineralogy: Thin outer calcitic and thick inner aragonitic layers.

Ecology and geography: Plicatulids are largely tropical, inhabiting water to a depth of 20 metres, (Yonge, 1973).

Taxonomic diversity: Monogeneric. Cox in Moore (1969) also included the genus *Atreta*. This is rejected here, see section 2.3.3.5. It would seem that fossil *Plicatula* were more abundant and speciose than in Recent times.

Geological range: Middle Triassic (Ladinian) - Recent Sepkoski (1982).

Discussion: The plicatulids first appear in the fossil record at the same time as the oysters. Therefore it would not seem unreasonable to suggest that these monomyarian bivalves may be of the same clade of cementers, the major division being based on the valve by which they cement. Such a relationship is, however, unfounded: the Plicatulidae have a grossly different shell microstructure and mineralogy, differ from the oysters in the construction of the hinge and ligament and have more primitive gills. The similarities between the two groups may be seen to result only from convergent evolution.

Pelseneer (1906) placed *Spondylus* and *Plicatula* within the same family within the Pectinacea. However, Watson's 1930 anatomical study on the plicatulids shows clearly that *Plicatula* is distinct from *Spondylus,* and indeed that the latter is more closely related to *Pecten* than to the former. Some of these differences, e.g. lack of a foot, and poorly developed velum might be attributed to *Plicatula* having had longer to adapt to the cemented habit than the spondylids, but others, such as the more simplified gills, different nervous system and lip apparatus and lack of pallial eyes cannot be reconciled with the plicatulids and the spondylids belonging to the same clade. This evidence also refutes Jackson (1890), who claims that *Plicatula* is a direct descendant of *Spondylus.*

Cox and Hertlein in Moore (1969) acknowledge the separateness of the plicatulids and spondylids, placing them in separate families, yet retaining them both within the Pectinacea. Yonge (1973) questioned this on the grounds of the distinct plicatulid ligament, and in 1975 elevated the Plicatulidae to a superfamily Plicatulacea along with the Dimyidae. He believed that the plicatulids had evolved from the Dimyidae. However Waller (1978) presents evidence on the ligament of both *Plicatula* and *Dimya* that suggests that the Dimyidae are more derived than the Plicatulidae, and elevates the former to a superfamily, Dimyacea. It is therefore clear that the Plicatulacea should be regarded as a distinct clade of cementing bivalves.

2.3.3.7 SUPERFAMILY ANOMIACEA Rafinesque, 1815

Valve of attachment: All attach with the right valve. Attachment is by way of a calcified byssal plug which passes through a large circular notch in the right valve, Figure 2.4. Secondary freedom has been acquired in two living genera; *Placuna* and *Enigmonia*, the latter being motile.

Figure 2.4: Deceased *Anomia ephippium* in Galway Bay, Eire. Note the persistence of the byssal plugs after death, even after the loss of the right valve. Rephotographed off colour slide.

Adductor musculature: Monomyarian with a distinctive array of byssal retractor and pedal muscles on the left valve, see Figure 2.5.

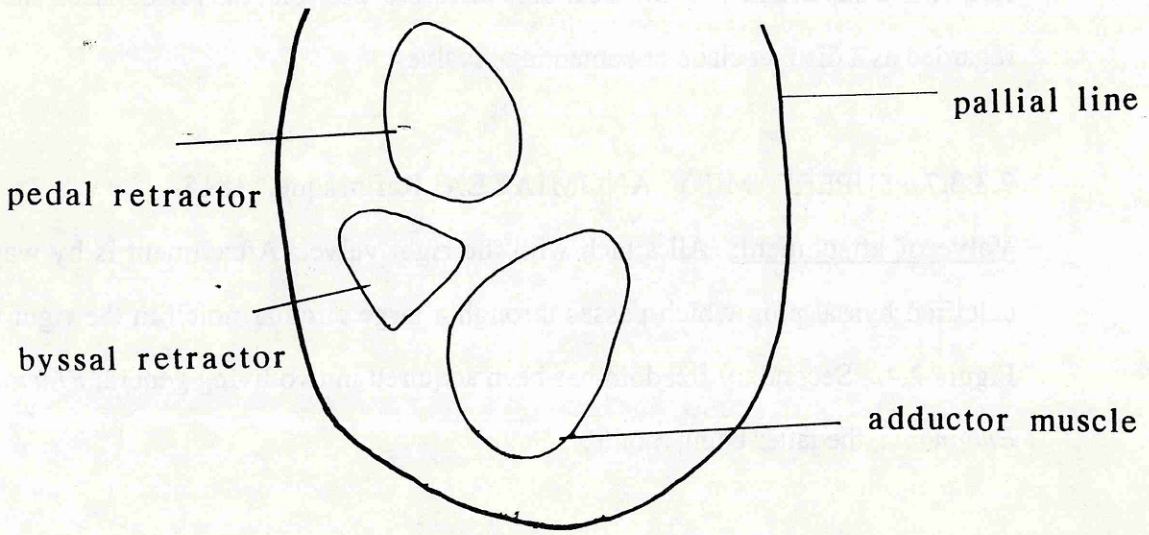


Figure 2.5: Musculature of the left valve of *Anomia ephippium*

Anatomical detail: The foot is retained. Mantle attachment is deeply inset towards the dorsal margins of the valves.

Valve morphology: Grossly dissimilar valves: inequivalve and inequilateral. The right valve is thin and virtually flat, punctured by an almost circular enclosed byssal notch, dorsally placed towards the umbo. The left valve is markedly convex and larger than the right. Xenomorphism is frequently displayed. Edentulous. Invaginated ligament held on crura.

Valve mineralogy: Outer calcitic and inner aragonitic layers.

Ecology: Modern *Anomia* and *Monia* live subtidally. (*Anomia ephippium* collected in Galway Bay were just exposed by the lowest water of the low Spring tides in April 1988.)

Taxonomic diversity: At least nine genera described.

Geological range: Jurassic (Upper Bathonian) - Recent, Fürsich and Palmer (1982). Earlier claims for anomiids are not substantiated, Fürsich and Palmer believing the majority to be misidentifications of *Placunopsis*. Newell and Boyd (1970) named a Permian bivalve *Permanomia texana*, under the impression that it was a Palaeozoic anomiid. Their figure (34,F) of the holotype shows an alleged byssal plug adhering to the left valve, however this is likely to be an artefact. My observations of dead anomiids suggest that decay of the soft parts leads to the left valve rapidly becoming dissociated from the plug, which remains attached to the substratum. Newell and Boyd failed to discover the right valve of *Permanomia*, which would provide the conclusive proof that it was an anomiid. There is a great taphonomic bias against the preservation of the right valves of members of the Anomiacea; the presence of the deep byssal notch and the fact that the valve is frequently exceedingly thin (Recent *Monia squama* - 100 μm) imparts mechanical weakness. As a result of this the fragile right valve is seldom found in palaeontological collections. Hasenmueller and Hattin (1990) report that of 500 specimens of Turonian anomiids collected in Kansas none

were of the right valve. Only the discovery of the right valve of *Permanomia* is likely to resolve its affinities.

Discussion: Using the definition of cementation given in section 1.2 the calcified byssal attachment seen in the majority of Anomiacea may be classified as cementation in the sense of this project. The persistence of the plugs long after death leads me to consider them permanently attached. However, it must be made clear that the mode of attachment displayed here is a result of modification of the byssal apparatus and not of the mode of shell secretion as seen in other cementing bivalves described herein.

There are reports that members of the superfamily are capable of shell cementation. Fürsich and Palmer (1982) describe the first proven anomiid, *Eonomia timida*, from the Bathonian of Normandy as attached by the right valve, but also possessing a byssal notch. However, I believe that this species did not cement by the 'lower' valve. Figure 2.6 shows a specimen of *E. timida*, collected from the Falaises des Vaches Noires (Oxfordian) in Normandy. Although this specimen appears to be attached to a gryphaeid oyster, thin sectioning reveals a thin (>20μm), but persistent layer of sediment between the valve and the substratum, see Figure 2.7. This feature is not isolated to this individual but has also been observed in the paratype JZ.1784 (OUM). The presence of an apparently functional byssal notch throughout life must also be taken as indicating that *Eonomia* did not shell cement.

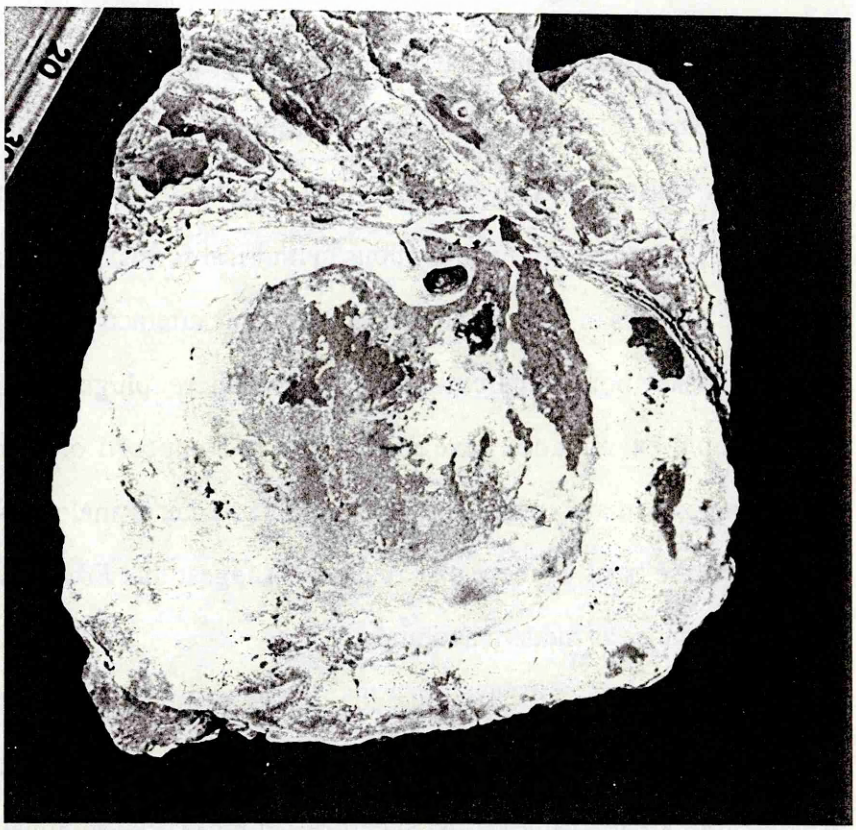


Figure 2.6: *Eonomia timida* apparently shell cemented. Specimen VN42. Rephotographed from colour slide.

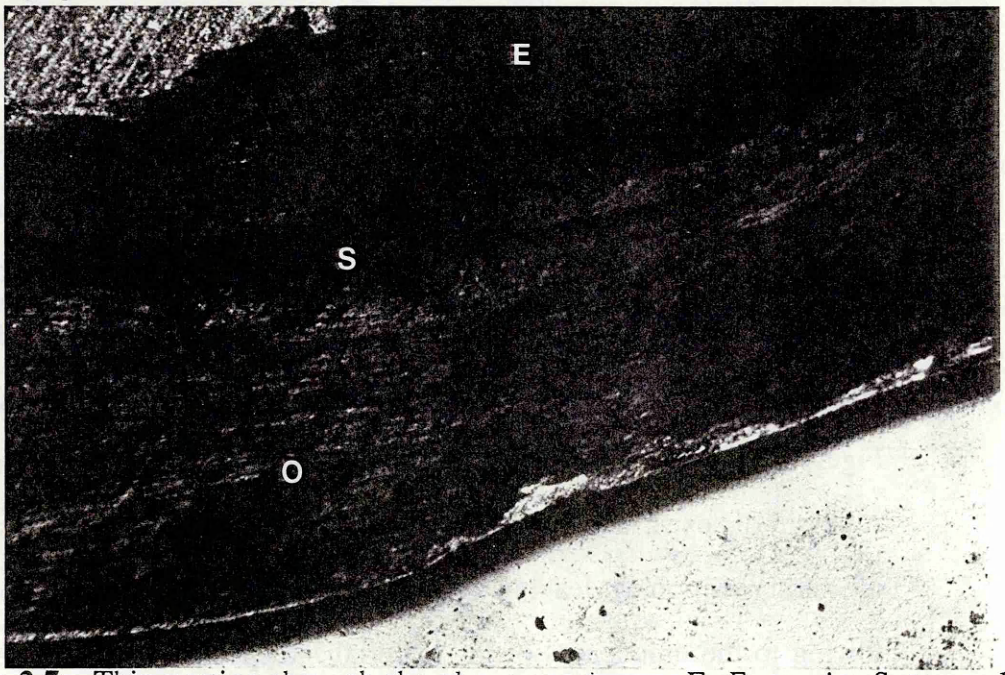


Figure 2.7: Thin section through the above specimen. E=*Eonomia*, S=trapped sediment and O=Oyster shell. Field of view=3.47mm. Thin section TS42.

Fürsich and Palmer found no trace of a byssal plug in *Eonomia*, implying that it was unmineralized. However, my examination of the collection housed at Oxford University Museum has revealed possible candidates for these features. Several of the substrates are encrusted by amorphous cylindrical forms. These may be interpreted as either the remains of byssal plugs or as diagenetic artefacts. Specimen J41088 attached to a plesiosaur bone apparently bears one of these 'plugs' within the byssal notch. Microscopic examination reveals that this is composed of many parallel ribbons, running approximately parallel to the shell height, i.e. is analogous to modern anomiid plugs. On the basis of these observations I suggest that *Eonomia timida* attached in the same manner as modern anomiids.

Fürsich and Werner (1988) report the certain presence of calcified byssal plugs in Upper Jurassic anomiids. Further examples of the mode of anomiid attachment in the fossil record are unavailable. As stated earlier the crucial right valve seldom preserves and the plugs very rarely figure in the literature, the latter probably because palaeontologists are not furnished with a search image for these most unbivalve-looking structures. However, investigation of Recent material has revealed possible convergence with the attachment of shell cemented bivalves. During the course of this study a large number of modern anomiids have been studied, both *Anomia ephippium* and *Monia squama*. Although the normal mode of attachment is the calcibyssus there is a single notable exception. A single specimen from a batch of 53 *Monia squama* attached to *Modiolus modiolus* dredged off Oban, was apparently shell attached (see Figure 2.8). It was not possible manually to dislodge the valve from the substratum. A byssus did exist, albeit poorly calcified. Unfortunately most of the specimen spalled off during sectioning, leaving a white powdery material adhering to the substratum, (owing to the uniqueness of the material the specimen was not embedded). The remaining cemented fragment has been deposited in NHZ (specimen LEO).

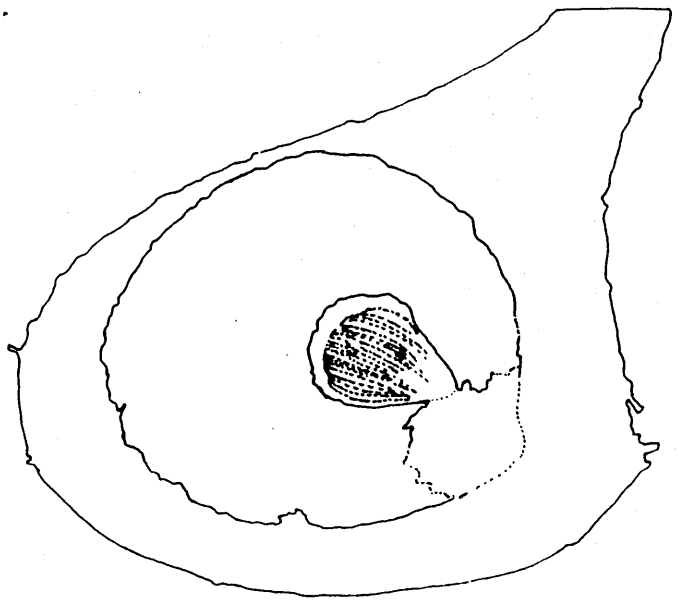


Figure 2.8: Right valve of *Monia squama* apparently shell cemented to *Modiolus modiolus*. Valve height=25mm.

Subsequently two similar examples of a shell cemented *Monia squama* have been identified in the collections of the NHZ, unregistered specimens of the Smith Collection. Interestingly a short abstract by Chace (1961) reports "an interesting freak *Anomia*" in the collections of the Natural History Museum, San Diego which cements by its upper valve. This again would seem to provide evidence that modern Anomiacea are capable of attaching by the valve as well as by a calcified byssus i.e. in the mode of *Eonomia*. Unfortunately Chace never figured or described his specimen elsewhere.

Yonge (1977) noted that the anomiacean genus *Placunanomia* (Miocene - Recent) "literally cemented to the substrate" by fusion of the byssal cement with the valve around the byssal notch. Inspection of the limited material of this genus in NHZ collections has failed to substantiate Yonge's claims.

2.3.3.8 SUPERFAMILY OSTREACEA Rafinesque, 1816

Valve of attachment: Modern oysters invariably attach by the left valve at a very early stage in ontogeny. Statements to the contrary by Yonge (1953, page 473) and J.E. Morton (1958, page 195) are clearly unfortunate oversights. Stenzel (1971) dismisses all claims for right valve cementing oysters as error of identification of the valves. There are four species of oyster in which cementation does not seem to occur; *Ilymatogyra arietina* (Cenomanian), *Odontogryphaea thirsae* (Spanarcian), *Exogyra tigrina* (Campanian) and some individuals of *Rhynchostreon suborbiculatum* (Cenomanian - Turonian).

The extent of attachment varies markedly even within species. In general, however, the Gryphaeidae have small attachment scars.

Adductor musculature: Monomyarian. Anterior adductor is lost in adulthood.

Anatomical detail: Adult lacks a foot,which atrophies immediately after settlement (Hickman and Gruffydd 1971 and Cranfield 1973a).

Careful dissection shows that the mantle is not attached to the valves at any point other than at the insertion of the adductor muscles. Stenzel (1971) refers to the genus *Saccostrea* as 'archaic' as he believes that it does possess a pallial line. However, in specimens that I have observed it is unclear whether this is true or whether it is the impression of the gill wheal. The mantle margins of oysters are comparatively simple with no pallial eyes.

The true oysters are characterized by the possession of Quenstedt's muscle which runs between the gills and an attachment site to the dorsal part of each valve. This muscle is believed to manipulate the gill and labial palp position, and probably to derive from the redundant pedal muscles (Galtsoff 1964).

Valve morphology: Oysters show the most remarkable plasticity of shell form; Gunter (1964, p.134) remarked 'within certain limits, defined by the fact that the shells consist of two hinged valves, oysters are among the most plastic organisms known'. The tremendous variation displayed in oyster shell morphology is in part

environmentally controlled, for example the effect of the substrate, crowding and current strength. The effect of substrate irregularity is paramount and may be reflected in xenomorphism of the right valve.

In most species the valves are highly inequivalve, the attached left valve being more convex. The right valve is frequently flat with less height than the left. The valves are frequently chambered and contain conchiolin sheets. Edentulous. Ventral migration of the hinge line with an amphidetic ligament. The ornament displayed is very varied, comprising commarginal flanges and hyote spines.

The families Ostreidae and Gryphaeidae may be distinguished on the following morphological criteria recognised by Stenzel (1971);

(i) The Gryphaeidae possess an orbicular shaped adductor scar as compared to the reniform scar in the ostreids. This scar is more dorsally positioned in the former group.

(ii) The Gryphaeidae generally have only a small attachment scar.

(iii) The Ostreidae possess a deep subumbonal cavity which is either shallow or absent in the Gryphaeidae.

[Further distinction is made between the families based on anatomical differences and reproductive strategy.]

Valve mineralogy: Entirely calcitic, apart from the myostraca and ligament fibres.

Ecology and geography: Modern oysters are found in all but the highest latitudes, and are capable of tolerating a range of salinities, from normal to brackish estuarine water. They also inhabit a range of depths from shelf seas to the intertidal, where they may encrust many substrata, including mangrove roots. Oyster larvae are gregarious (Bayne 1969) and hence able to form 'reef' accumulations, for example the Tertiary *Crassostrea* reefs described by Littlewood and Donovan (1988).

Taxonomic diversity: High. Stenzel records 20 genera of Gryphaeidae, of which only two, *Hyotissa* and *Pycnodonte,* are extant, and 20 genera of Ostreidae of which six

are still extant; *Ostrea, Crassostrea, Saccostrea, Lopha, Alectryonella* and *Striostrea.* Of these many different sub genera have been described.

Geological range: Late Triassic (Carnian) - Recent (Stenzel, 1971).

Discussion: The oysters must be regarded as amongst the most successful cementing bivalves. Their long geological history, their high taxonomic diversity, wide distribution and ability to form 'reefs' attest to this. Yet the origin of the group is obscure. Many authors have sought to identify the ancestral oysters, for example Nakazawa and Newell (1968), Newell and Boyd (1970 and 1989) and Stenzel (1971). This task has been hampered by the poor fossil record of early oysters, confusion induced by the 'simultaneous' appearance of cementation in other unrelated groups e.g. Plicatulacea, Dimyacea and the Terquemiidae, and an ignorance of exactly how oysters attach.

As noted in Section 2.3.3.1 I believe that the evidence that the oysters derived from pseudomonotids, as suggested by Newell and Boyd (1970), is equivocal. Lack of any direct evidence, coupled with major differences in the valve of attachment, valve microstructure and pre-attachment stages are major obstacles to accepting their proposals.

Stenzel (1971) maintains that the oysters are diphyletic, with the Ostreidae and Gryphaeidae having separate origins. He bases this conclusion on the biogeographic distribution of the first appearances of each family. He records the Gryphaeidae as first appearing in the Arctic, as *Gryphaea* in the Carnian and *Liostrea* in the Norian, whilst the Ostreidae are first represented by *Lopha* in the Mesogean/Pacific region during the Carnian. He states (p.N1056) "Great geographic distance between the places of origin of *Gryphaea* and *Lopha* are believed to be indicative of diphyletic origins." However, disparate geographic distribution in the marine environment is a poor primary argument for diphyly. Particularly since, as Nicol (1984) points out, Stenzel himself admits that Triassic *Lopha* are difficult to distinguish from terquemiids and pseudomonotids. On these grounds Nicol (1984) rejects Stenzel's assertion and

suggests that the Ostreidae is a geologically younger family, derived from the Gryphaeidae in the Middle Jurassic.

Stenzel backs up his argument for a diphyletic origin by recording features which he believes illustrate the distinctiveness of the two families. However, I believe that the evidence he cites is actually indicative of the derivation of the ostreids from the more primitive gryphaeids. These points are discussed below:

(i) *In the Recent Gryphaeidae the intestine passes through the pericardium and the ventricle whilst in the Ostreidae the intestine bypasses the heart.*

Pelseneer (1906) found that penetration of the heart by the intestine is the normal primitive condition in bivalves. This would tend to suggest that the ostreid condition is derived.

(ii) *All modern Gryphaeidae are non-incubatory, whilst of members of the Ostreidae are incubatory.*

Here again non-incubatory reproduction is the norm for most bivalves and is considered the primitive condition. Not all ostreids are incubatory; genera such as *Arctostrea, Crassostrea* and *Saccostrea* are nonincubatory (Galtsoff, 1964).

Further evidence of the derived nature of the ostreids may be gained by study of the prodissoconchs. Stenzel (1971, p.N1009) illustrates the larval shells of members of both families. The larvae of gryphaeid Pycnodontinae have five hinge teeth evenly spaced. By contrast members of the Ostreidae have only four hinge teeth arranged in pairs with a significant gap between. One might also argue that the large attachment area of ostreids is derived with respect to the small area, restricted to early growth stages, found in gryphaeids. Moreover, Hudson and Palmer (1976) report that the Lower Liassic gryphaeid *Liostrea hisingeri*, despite certainly belonging to the Gryphaeidae, has certain intermediate features with the ostreids, e.g. small promyal chamber.

The Gryphaeidae and Ostreidae have a number of highly specialised shared characters which also tend to suggest a common origin. These include very derived shell

microstructure and mineralogy, sinistrally pleurothetic orientation and the possession of chomata and the Quenstedt muscle.

My conclusion is that the there is no evidence that the oysters are diphyletic. In this study both oyster families will be considered a single clade.

2.3.3.9 Subclass PALAEOHETERODONTA
Order UNIONOIDA
Superfamily UNIONACEA
FAMILY **ETHERIIDAE** Swainson, 1840

There are three genera of cementing freshwater bivalve to be considered; *Etheria, Acostaea,* and *Pseudomulleria.*

Valve of attachment: All genera may attach by either right or left valve; specimens of *Etheria elliptica* observed in the NHZ were observed to be equally split between the two categories, for example lots 54.12.28 and 54.12.28.1, obviously collected from the same unknown locality. Of the nine individuals, five attach by the right and four by the left valve. A similar grouping, unregistered, from the Kangera River, Uganda, were found to comprise three right and three left valve cementers. This would seem to indicate that even within a specific population there is a genuine ability to cement by either valve and that the local gene pool does not have a predisposition one way or the other.

All genera attach at a comparatively late ontogenetic stage and do so for the full extent of the attached valve.

Adductor musculature: *Etheria* is dimyarian with two muscle scars of approximately equal area but of differing shape, the posterior being reniform and the anterior more elongate. *Acostaea* and *Pseudomulleria* are both monomyarian. I have insufficent observations to tell if the remaining muscle is the anterior or the posterior.

Anatomical detail: A number of specimens of preserved *Etheria elliptica* from Zaire were loaned to me from the Muséum National d'Histoire Naturelle by P. Bouchet for dissection. No foot was discovered. The mantle margins are simple, unfused and thick. There is no discrepancy in the thickness between the mantle margins of the cemented and non cemented valve as noted by Yonge (1967b) for *Chama*, (another cementer on indifferent valves).

Valve morphology: The unattached juveniles were observed by Yonge (1962a,1978a) to be equivalve. The adults are characterised by a great morphological plasticity equal to that of the oysters.

Etheria elliptica is subequivalve, and highly distorted to conform to the substrate. No xenomorphism has been observed. Inequilateral, the umbones located to the anterior. Edentulous. Amphidetic hinge line with the ligament set into a deep pit which bisects the area. Certain specimens show much ventral migration of the hinge line on the attached valve. The valves are greatly extended ventrally and may attain large shell heights, e.g. NHZ specimen 58.8.11.1 exceeds a shell height of 500mm. A characteristic thick green periostracum is often severely corroded to reveal the nacreous, often chambered, shell below. The chambering within the shell may cause blistering on the internal face of the valves. External valve ornament varies markedly from smooth with faint commarginal ridges to those having hyote spines.

The genera *Acostaea* and *Pseudomulleria* are essentially similar but with less ventral extension and a more triangular appearance, there being an anterior reduction of the valves. *Acostaea* possesses a spatulate anterior spur. Ligament is opisthodetic. No hyote spines have been observed.

Valve mineralogy: Exclusively aragonite.

Ecology and geography: All are entirely freshwater bivalves found only in tropical river systems. Each genus has a very restricted geographic range (see Figure 2.9), *Etheria* being restricted to the Congo and Nile basins and Madagascar, *Acostaea* to the

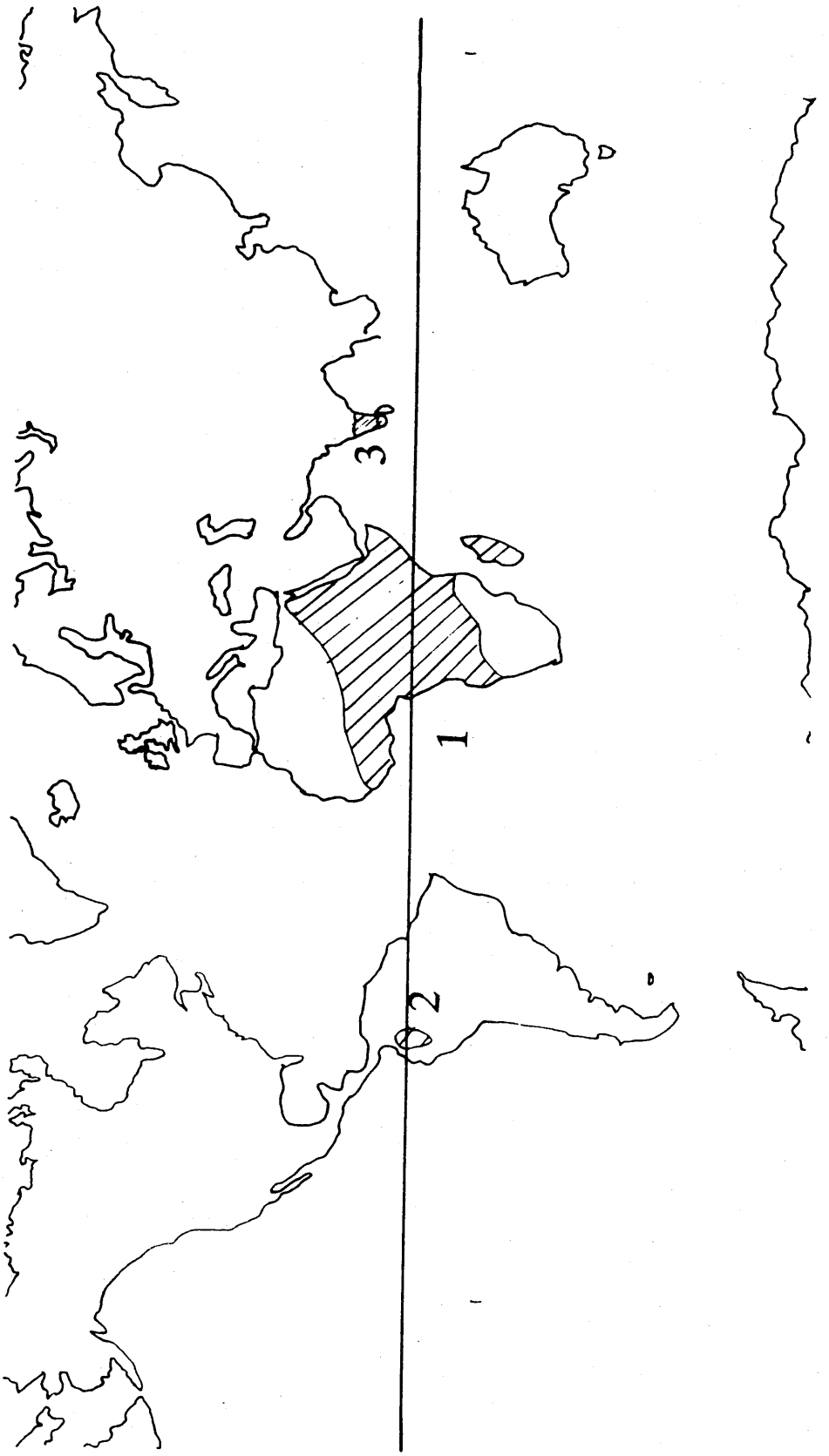


Figure 2.9: Biogeographic distribution of members of the Etheriidae. Information from Pilsbury and Bequaert (1927) and Yonge (1962b and 1978a). 1=*Etheria*, 2=*Acostaea* and 3=*Pseudomulleria*.

River Magdalena in Colombia, South America, and *Pseudomulleria* to the Mysore district of southern India.

Etheria is able to produce reefs (Yonge 1962a); there are no such reports for either of the other two genera. Formerly, *Etheria* was widespread in central Africa and formed an important part of the diet of river tribes (Pilsbury and Bequaert 1927), but today it is rare, only occurring in the more inaccessible parts of the rivers (personal communication - Jonathon Carter Reid, Nigeria).

Taxonomic diversity: Hass in Moore (1969) states that there are four genera of cementing etheriid. However his inclusion of the genus *Bartlettia* would seem to be erroneous. Parodiz and Bonetto (1963) believe it to be not an etheriid but probably a mutelid. In any case the genus does not cement but wedges itself in crevices (Yonge 1978a). The remaining genera appear to be monotypic.

Geological range: *Etheria* is recorded from the Pliocene to Recent. *Acostaea* and *Pseudomulleria* are only recognised in the Recent.

Discussion: The Etheriidae are unquestionably members of the Unionacea. Gregoire (1974) and Yonge (1978a) consider that they are most likely to have evolved from the family Unionidae by the adoption of the pleurothetic attitude followed by cementation. Boettger (1933), however, considered their ancestry to lie amongst the Mutelidae. The Unionidae option is more likely as Gregoire shows that the organic matrix in the shell of *Etheria* closely resembles those of *Unio*, and is unlike that of mutelids, whilst Yonge has evidence that the etheriid gills are of unionid type and that etheriids possess a glochidium type larva. The evolution of the cemented habit from a unionid stock is problematic to envisage, however, as the genera of that family are exclusively burrowing with no evidence that there is ever any byssate attachment. The preservational potential of epifaunal freshwater bivalves is poor, compared to their marine counterparts. The likelihood of burial prior to breakage is small and the acidic nature of freshwater is liable to promote shell dissolution. These factors, coupled with the restricted geographic distribution of the etheriids make it unsurprising that their

fossil record is poor. However, one might expect that at least the attached 'lower' valve would appear in the fossil record more often than the valve of byssate freshwater bivalves (e.g. *Dreissena* of the superfamily Dreissenacea). It is probably therefore safe to accept the first appearance date given by Hass in Moore (1969) as Pliocene.

How many times has the cemented habit evolved within the etheriids? It is an important question whether the three genera separately acquired the ability to cement, and so their similarities are therefore convergent, as suggested by Anthony (1907) and Prashad (1931), or whether they have have a common cementing ancestor and that the differences in musculature and morphology are divergent, as argued by Yonge (1962a). In the former case we would have to concede that the Etheriidae is a polyphyletic grouping.

The modern distribution on three separate continents (see figure 2.9) is persuasive that the three are independent clades. The only way to reconcile this distribution with a single clade is to suggest that the Etheriidae are an older group than the fossil record implies, dating back until at least the Late Jurassic.

During the Late Jurassic S. America, Africa and India were all closely spaced as part of the supercontinent Pangaea (Smith and Briden, 1977). A single innovation of the cemented habit could potentially have spread across the landmass with exponents becoming separate after supercontinent breakup. This hypothesis in my view is exceedingly unlikely because;

(i) there are no record of fossil etheriids prior to the Pliocene.

(ii) there is no reported evidence of etheriids in intermediate geographical locations.

If the etheriids genuinely did evolve in the Pliocene we surely cannot invoke a single origin. Isolation in the freshwater habitat usually acts as a barrier to stop innovations spreading intercontinentally. In addition to this argument it must be noted that the unionids are tremendously plastic in their morphology and have evolved many adaptations over and over again (S. Morris - personal communication). The very fact that the unrelated *Bartlettia* has shown some convergence with the etheriids seems to

demonstrate this. It is therefore most likely that the etheriids are polyphyletic and that the unionids have evolved the cemented habit three times.

Skelton (personal communication) has brought to my attention the possibility of another mechanism of transfer of a single cemented form between continents. He suggests that glochidium larvae may be transported by avian agents, such as cattle egrets. Attractive though this may seem, further evidence is required as to whether the glochidia can attach to birds. It should, however, be noted that glochidium larvae do attach to fish gills (Yonge, 1978a).

2.3.3.10 Subclass HETERODONTA

Order VENEROIDA

SUPERFAMILY **CHAMACEA** Lamarck, 1806

Valve of attachment: Members of the Chamacea may cement by either left or right valve. Odhner (1919) split these into two separate taxa; *Chama*, which attaches by the left valve and *Pseudochama*, which attaches by the right. Nicol (1952) observed that *Echinochama* (Miocene - Recent) is pleurothetic almost exclusively on the right valve, out of 1000 specimens only 1 lying on its left valve. In other species, however, it is clear that attachment is by either valve (Yonge 1967b, Kennedy, Morris and Taylor 1970, and personal observation).

Secondary freedom has been acquired in the genus *Echinochama*, which rests on its spines on a gravel substrate as an adult.

Adductor musculature: Isomyarian.

Anatomical detail: Small but active foot. The inner mantle folds are fused to form short siphons and there is a pedal gape. The middle mantle lobes have a fairly well developed sensory tentacles, but no pallial eyes. Yonge (1967b) reports that the mantle lobes are asymmetric, those on the attached side of the body being thicker than those on the non attached.

Valve morphology: Inequilateral, thick coiled prosogyrate valves. Varies from being equivalve e.g. *C. gryphoides* (Allen, 1976) to highly inequivalve. In the latter case the unattached valve is virtually flat. Parivincular ligament, split anteriorly. At least one cardinal tooth in each valve. The pallial line is broad and entire. Ornament varies from squamous flanges e.g. *C. lazarus* to long pointed spines e.g. *Echinochama*. I have observed no xenomorphism.

Valve mineralogy: The majority of chamids are wholly aragonitic. Two exceptions are *C. pellucida* and *C. exogyra*, which live in cooler waters, and which have calcitic outer shell layers (Kennedy, et al. 1970).

Ecology and geography: Tropical- subtropical. Inter- to shallow sub-tidal, often in association with reefs.

Taxonomic diversity: The literature is somewhat confusing, still regarding *Chama* and *Pseudochama* as separate genera.

Geological range: Upper Cretaceous (Senonian) - Recent (Kennedy et al. 1970).

Discussion: Odhner (1919) and Yonge (1967b) implied that the Chamacea are closely related to the extinct cementing rudists. The similarities lie in the coiled shell form, the indifferent cementation by either valve, and a similar dentition. If the Chamacea were derived from the rudists then they would not be considered as an independent clade of cementing bivalve. However, Kennedy et al. (1970) dismiss the similarities with the rudists as convergent, a view with which I concur. They exhaustively examined the superfamily in relation to putative ancestor groups put forward by other authors (referenced therein); the Carditacea, Lucinacea, Crassatellacea, Veneracea, Cardiacea and the rudists. They found that the only possible close relatives were the Lucinacea and the Carditacea, of which the Lucinacea were discounted because of their burrowing habit. The Carditacea share the same shell structure as the chamids,have a similar dentition and many carditacean species are byssate and inequivalve. Kennedy et al. suggest that the Chamacea derived in the Upper Cretaceous from a byssate *Cardita*, citing *Cardita beaumonti var. amelliae*, from the Upper Cretaceous of Iraq as

a likely member of the ancestor group. In this case it is possible to regard Chamacea as a distinct clade of cementing bivalve.

2.3.3.11

Order HIPPURITOIDA

SUPERFAMILY **HIPPURITACEA** Gray, 1848

* Virtually all information used to compile this section is derived from Skelton (1976,1978). There was no need to replicate his observations whilst there were other less well investigated clades.

Valve of attachment: Variable within the superfamily. The Diceratidae may cement by the left or the right valve, but do so consistently within a genus, e.g. *Epidiceras* invariably attaches by the left and *Diceras* by the right valve. The Requieniidae all attach by the left, whilst the remaining families all cement by the right.

Adductor musculature: Dimyarian, muscles frequently attached to myophores. Heteromyarian, the anterior being larger than the posterior.

Anatomical detail: Skelton indicates that there were no pedal retractor muscles and hence the likelihood that the rudists lacked a foot.

Valve morphology: Subequivalve to inequivalve, the later rudists being progressively more inequivalve. The attached valve is larger than the often operculate unattached valve. Shell walls are thick and well ballasted. The Diceratidae and Requieniidae have external ligaments and coiled spirogyrate valves, whereas the later rudists had invaginated ligaments which allowed uncoiled growth. Skelton (1976) refers to the rudists displaying xenomorphism, but the term is not used in its true sense as defined by Stenzel (1971). Large pachydont teeth. Skelton (personal communication) maintains that the rudists lack a pallial line and that attachment of the mantle to the valves was by way of isolated patches of myostracum. Valve ornament includes radial ribbing.

Valve mineralogy : Outer calcitic and inner aragonitic layers. In the radiolitids the outer calcitic layer is greatly developed and cellular in texture.

Ecology and geography: Widespread in Tethyan shelf seas, able to form large biogenic accumulations.

Geological range: The superfamily extends from the Upper Jurassic (Middle Oxfordian) to the Danian, although the majority became extinct in the Upper Cretaceous (Maastrichtian).

Taxonomic diversity: Skelton (1978) describes seven families of rudists, see his Figure 17.

Discussion: The rudists are a distinct clade of cementing bivalves. The ancestor group is widely inferred to be the Megalodontidae. The megalodonts are largely equivalve and spirogyrate, composed entirely of aragonite. Skelton (1976) shows the presence of pedal retractor muscle scars and suggests that at least the juvenile growth stages may have been byssally attached, although the heavily ballasted shell of the adults may have been free living.

The first recorded rudists, the diceratids, occur over a wide geographic area (Old World Tethys) already with the ability to cement and with an outer calcitic shell layer. It is not unsurprising that the orthothetic megalodontids, once preadapted to cement, should have been able to give rise to morphs able to cement on either valve, depending on which valve they became pleurothetic on. However, it is surprising that the first cementers should be taxonomically distinct as right or left valve cementers; yet Skelton (1976) is sure of that distinction on the basis of dental and size criteria. The expected scenario would be that seen in the Chamacea and the Etheriidae, with the orthothetic stage falling on either one valve or the other and cementing, with both morphs being demonstrably the same species. One might predict, therefore, that perhaps the cemented habit evolved twice within the Hippuritacea.

Subsequent radiation of the rudists from these earliest forms led to the evolution of the Requieniidae, an exclusively left valve cementing form, in the Tithonian from

Epidiceras; and a multitude of other right valve cementing families, derived from *Diceras*, see Skelton's (1978) Figure 17.

2.3.3.12 Subclass ANOMALODESMATA

Order PHOLADOMYOIDA

Superfamily PANDORACEA

FAMILY **CLEIDOTHAERIDAE** Hedley, 1918

Valve of attachment: Attachment is invariably by the anterior half of the right valve.

Adductor musculature: Heteromyarian. The anterior adductor is always at least twice the size of the posterior.

Anatomical details: Dissection of preserved specimens of *Cleidothaerus albidus* shows that the foot is particularly small. Morton (1974) refers to it as inactive in the living animal. The mantle margins are fused to produce inhalant and exhalant siphons.

Valve morphology: Grossly inequivalve and inequilateral. The cupped right valve is basically a V shape in section resting on one limb. The left valve is a flat operculate structure, bearing a single cardinal tooth and a lithodesma. Both valves are spirally coiled. The pallial line is entire, and unusually for the superfamily Pandoracea, lacks a pallial sinus. Maximum shell height 80mm.

Valve mineralogy: Exclusively aragonite.

Ecology: The family is entirely Australasian. Morton (1974) describes it as found only in the sublittoral fringe, particularly attached to algal holdfasts.

Taxonomic diversity: This family is monogeneric, with an Australian and a New Zealand species, *Cleidothaerus albidus* and *C. maorianus* respectively. However, Yonge and Morton (1980) consider that these may be synonyms.

Geological Range: Miocene - Recent. The first recorded appearance is in the Awamoan, Late Miocene, (Finlay and Marwick, 1940).

Discussion: The independent occurrence of the cemented habit in *Cleidothaerus* and in the Myochamidae is discussed in section 2.3.3.13, in connection with the latter group.

Cleidothaerus bears a striking similarity to the Chamacea, in particular to spineless '*Pseudochama*', indeed Lamarck placed *C. albidus* in the genus *Chama* (Lamy 1935). Such similarity, however is purely convergent. The two genera have entirely different shell structures (see Appendix 2), dentitions and detailed morphology, their similarities resulting from coiling and cementation. There is no reason to invoke a close evolutionary link between these two families.

2.3.3.13 Family MYOCHAMIDAE

GENUS *MYOCHAMA* Bronn, 1862

Valve of attachment: Cementation is by way of the entire surface of the right valve.

Adductor musculature: Isomyarian.

Anatomical detail: Dissection of *Myochama anomioides* revealed no trace of a foot; however Yonge and Morton (1980) do note its presence as a small organ with no observable function. The mantle margins are fused with short siphons.

Valve morphology: Small valves <15mm shell height. Inequivalve and inequilateral. Triangular shaped. The right attached valve is flat, slightly shorter than the left valve which is highly convex. The pallial line is entire, with a posterior pallial sinus. A single hinge tooth and a lithodesma. The left valve is strongly ribbed after 2mm shell growth, although this ornamentation is often obscured by strong xenomorphic ornament.

Valve mineralogy: Exclusively aragonite.

Ecology: *Myochama* is limited to the coasts of South East Australia, including Tasmania. It is exclusively found cemented to the valves of living *Glycymeris keppeliana, Eucrassatella kingicola,* and *Neotrigonia margaritacea*, see Figure 2.10.

Attachment is always to the posterior portion of the host valves. Although Yonge and Morton (1980) discount any commensalism in this relationship, the specificity is so great that the possibility must not be excluded.

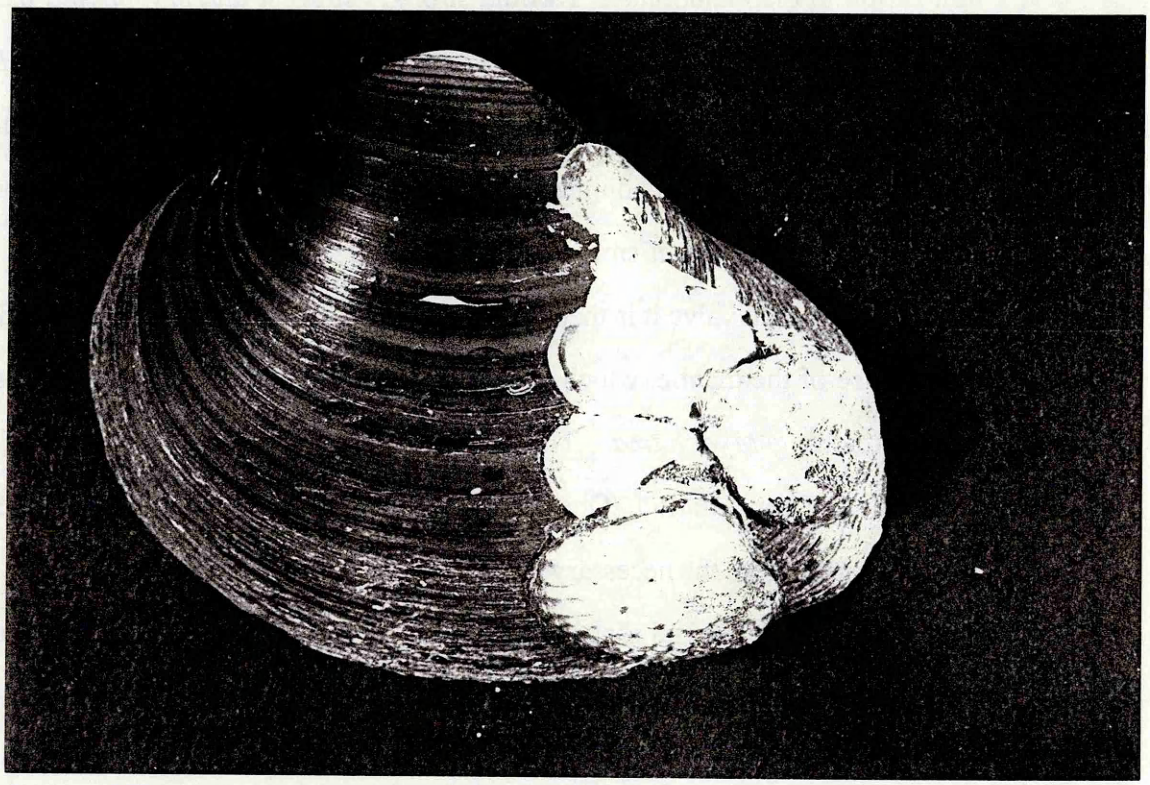


Figure 2.10: *Myochama anomioides* attached to the posterior of *Eucrassatella kingicola*. ex NHZ specimen collected from Twofold Bay, New South Wales, Australia. Height of *Eucrassatella*=c.60mm.

Geological range: Miocene to Recent.

Taxonomic diversity: Monogeneric.

Discussion: Cementation in the Myochamidae has arisen at the generic level, and is very much a side line, the remaining genera, *Myadora* and *Hunkydora* are sluggish shallow burrowers. The only morphological difference between the genera is the valve asymmetry. Whilst *Myochama* has a flat right and a convex left valve, *Myadora* and *Hunkydora* have a flat left and a convex right valve. The dentition remains the

same in both groups. In effect the cementers are a mirror image of the burrowers. Examination of the families within the Superfamily Pandoracea shows that whilst some are virtually equivalve eg. Thraciidae, Laternulidae and the Lyonsiidae, all the remainder are highly inequivalve. Only the genus *Myochama* has a flatter right valve. Thus the valve asymmetry displayed in the Myochamidae is seen to be a unique innovation in the Pandoracea. I would strongly suggest that *Myochama* has derived from inversion of *Myadora* in a restricted geographical area. (The genus *Myadora* appears earlier in the fossil record, in the Lower Oligocene and has a much wider distribution.) Such inversion may be accommodated by a single mutation, and is not unknown in other organisms, e.g. flounders (Hubbs and Hubbs 1945). Having attained a flat right valve it is then possible that the animal could exploit preadaptations in that lobe of the mantle, which allowed cementation. There are no records of a left valve-attaching *Myochama*. This suggests that inversion took place prior to the acquisition of cementation. One might predict that the left mantle lobe of the family Myochamidae lacks the necessary preadaptations for cementation.

The similar geographical distribution and common membership of the Pandoracea may make it attractive to link the the evolution of the Cleidothaeridae and the Myochamidae. The general biology of the two families has been little studied. Prior to the works of Yonge and Morton there is no published information since Hancock (1853a,b). However, it is clear that cementation has arisen independently in both these families. Morton (1977) perceives an evolutionary trend in the Pandoracea towards a more sedentary lifestyle. The evolution of cementation in these two families must be seen to be the culmination of this trend. They share little in common except for the cemented habit and the diagnostic shell structure of their superfamily. Morphologically they are highly distinct. In many respects the cleidothaerids are considerably derived with respect to the primitive pandoracean form, in the lack of a pallial sinus, coiling and the associated heteromyarianism. Yet the two families achieved cementation at virtually the same time in the fossil record. According to

Yonge and Morton (1980) the Cleidothaeridae appear slightly earlier in the Miocene; unfortunately I have been unable to obtain fossil material in order to examine early forms. The coincident appearance of the cemented habit in the families may relate to a very strong extrinsic factor, either in terms of a direct selection pressure or an environmental change, operating in the Miocene in the Australasian region. This will be discussed in Section 4.5.2

There now follow the descriptions of two possible cementing bivalve clades which have uncertain taxonomic position and are poorly known.

2.3.3.14. ?FAMILY **LITHIOTIDAE** Reis, 1903

The Lithiotidae are only recognised from two genera *Lithiotis* and *Cochlearites*, from the Lower Jurassic (Liassic) and are the subject of an extensive monograph by Reis (1903). His plates show that the valves are moderately inequivalve, edentulous, not dissimilar to the oyster *Crassostrea*, attaining a large size - 250mm shell height. The area is large with a migrated hinge line, and there is no median ligament groove. Cox in the *Treatise* (N1199) states that the attachment is probably by the right valve, whilst Chinzei (1982) claims that *Lithiotis* cements by the right valve and *Cochlearites* by the

left. Monomyarian. The shell is composed almost entirely of calcite and is frequently chambered. Chinzei (1982) suggests that the inner shell is composed of calcite, whilst the outer shell layers are aragonitic. However there must be some doubt as to Chinzei's observations; there are no other bivalves known to me in which this arrangement of shell mineralogy exists. It would seem that the lithiotids were capable of forming large bioherms, (Nauss and Smith, 1988).

Reis believed that the lithiotids were 'toothless spondylids', possibly implying that they belonged to the group now called terquemiids. This is, however, unlikely as they lack the pectiniform early growth stages and have a different shell structure.

Another possibility is that the lithiotids are right valve cementing oysters. The general shell form and mineralogy would seem to support this. However the lack of a median groove would seem to be an important distinguishing feature, and Cox, in Moore (1971), was unable to express a firm opinion as to their taxonomic position. Chinzei (1982) regards the lithiotids as members of the Pteriina. I have been unable to acquire any reasonable material for this study and thus must rely on the observations of others. Although like oysters in general shell form, it seems safest to exclude them from that clade.

2.3.3.15 FAMILY **CHONDRODONTIDAE** Freneix, 1959

The chondrodonts were originally described by Stanton (1901) as inequivalve, thick shelled, oyster-like bivalves. They range from the Hauterivian to Campanian (Cretaceous), Skelton (personal communication). They attach by the more convex valve, believed by Freneix and Lèfevre (1967) to be the right and by Douvillé (1902) to be the left(?). They are dimyarian, with a highly inset pallial line. Edentulous, with a triangular shaped area bearing chondrophores.

These bivalves are clearly not ostreid. The taxonomic position of the group is uncertain, having been variously shuffled from the Pinnacea (Douvillé 1902) to the Pectinacea (Stanton 1901, 1947). Even their description as cementing is in doubt. Both Stanton (1901) and Cox in Stenzel (1971) regard them as cementing bivalves; Skelton (personal communication) believes them to be byssate, whilst N. J. Morris (personal communication) believes that only the early representatives cemented.

2.3.4 Rejected claims for cemented bivalves

There are a small number of bivalves for which various authors have claimed the cemented habit, but examination of these forms for this study has rejected these assertions.

2.3.4.1 *Claraia*

Newell in Moore (1969) N337 claims that the genus *Claraia* of the family Aviculopectinidae cements on the right valve. The genus is a relatively abundant Lower Triassic bivalve, with biostratigraphic importance, described by Bittner in 1901. Examination of over 146 specimens in the NHP and Bittner's original figure (his Plate 8, figure 32) have failed to produce any evidence of cementation. Poorly preserved, squashed specimens may give the impression of distortion due to attachment. However, in isolation, distortion is not an acceptable criterion for cementation. Perfectly preserved specimens with no distortion e.g. LL15720, LL10216, LL16442, L58294-7 clearly did not cement.

2.3.4.2 *Pedum*

Hertlein in Moore (1969) implies that this pectinid genus cements and places it within the polyphyletic cementing *Hinnites* group. However, Yonge (1967a) clearly shows that these scallops are byssally attached within living scleractinians and examination of material at the NHZ confirms this. However the role that this habit may play in the acquisition of cementation is discussed in 5.3.

2.3.4.3 Clavagellacea

Morton (1974) regards the Clavagellacea as cementing bivalves. The adults occupy calcareous tubes, constructed by the siphons as a burrowing adaptation, to which one valve is fused. It is apparently unclear how this fusion takes place, but attachment of this nature does not fall within the definition for cementation used in this study.

CLADE	LEVEL	VALVE OF ATTAC-HMENT	FOOT	MUSCUL-ATURE	MINERALOGY*	HABITAT	EARLY BYSSATE STAGE?	RANGE
'PSEUDOMONOTIDS'	Generic	Right	?	Mono	C/A?	Marine	Y	Lo Carb - Up. Perm
HINNITES	Generic	Right	Y	Mono	C/A	Marine	Y	Miocene -Recent
CHLAMYS PUSIO	Species	Right	Y	Mono	C/A	Marine	Y	Recent
'EOPECTEN'	?Generic	Right	?	Mono	C/A	Marine	Y	Jurassic(Baj.-Bath?)
PROHINNITES	Generic	Right	?	Mono	C/A	Marine	Y	Cret (Val-Apt)
SPONDYLIDAE	Generic	Right	Y	Mono	C/A	Marine	Y	Jurassic (Baj.)-Recent
TERQUEMIIDAE	Family	Right	Y	Mono	C/A	Marine	Y	Lo. Perm.(?) - U. Jurassic
DIMYACEA	Family	Right	N	Di	C/A	Marine	N	Up. Trias-Recent
PLICATULACEA	Super family	Right	N	Mono	C/A	Marine	N	Mid. Trias-Recent
ANOMIACEA	Super family	Right	Y	Mono	C/A	Marine	Y	Jurassic-Recent
OSTREACEA	Super family	Left	N	Mono	C	Marine	N	Up. Trias-Recent
ETHERIA	Generic?	Right/Left	N	Di	A	Freshwater	N	Pliocene-Recent
ACOSTAEA	Generic?	Right/Left	N	Mono	A	Freshwater	?	?Recent
PSEUDOMULLERIA	Generic?	Right/Left	?	Mono	A	Freshwater	?	?Recent
CHAMACEA	Super family	Right/Left	Y	Di	A 2 sp C/A	Marine	Y	Up. Cret-Recent
HIPPURITACEA	Super family	Right/Left	N	Di	C/A	Marine	?	Up. Jur (Ox.)-Up. Cret(Maas.) (+few Danian)
CLEIDOTHAERIDAE	Family	Right	Y	Di	A	Marine	?	Miocene-Recent
MYOCHAMA	Generic	Right	Y	Di	A	Marine	N	Miocene-Recent
LITHIOTIDAE	?Family	Right	?	Mono	?C	Marine	?	Jurassic (Lias)
CHONDRODONTIDAE	?Family	?Right	Y	Di	C/A	Marine	?Y	Cret. (Haut.-Camp.)

Table 2.1: Summary of the information given in Section 2.3.3. Y=Yes, N=No, C=Calcite, A=Aragonite and *excludes myostraca and ligament.

2.4 OVERVIEW OF INFORMATION

Table 2.1 summarises the most important data given in the preceding section, 2.3.3, for each of the twenty clades of cementing bivalve recognised in this study. The material presented here will in effect serve as background data used in the following chapters. However, a number of points can be seen immediately from examination of the material presented here.

2.4.1 Taxonomic diversity of cementing bivalves.

The cemented habit has evolved in many different groups of bivalves. Although twelve clades are pteriomorphs, the remainder are scattered amongst the Unionacea, the heteroconchs and the anomalodesmatans. The estimate of the number of clades may be conservative since it does not account for possible multiple acquisition in the pseudomonotids, nor is it able to predict the occurrence of hitherto undiscovered cementers. The recent discoveries of *Eonomia* by Fürsich and Palmer (1982) and *'Eopecten'* highlight the fact that early Mesozoic cementing or apparently cemented bivalves may be misrepresented in the literature as oysters.

2.4.2 Anatomical considerations

There is obviously no set body plan for cementing bivalves. Adductor musculature may be mono- or dimyarian; the mantle margins may be very well developed or very simple; a foot may be present, reduced or absent and the basic valve form may have infinite variety. Most cementing bivalves cement on the right valve, others may cement on either valve, whilst only the oysters attach invariably on the left valve.

2.4.3 Geographical distribution

From the data in each of the preceeding sections it would appear that most of the cementing bivalves inhabit shallow waters, concentrated at lower latitudes. The implications of this for the evolution of the cemented habit will be discussed in Section 4.5.2.

2.5 CONCLUSIONS

1] The cemented habit in the Bivalvia has arisen at least 20 times.

2] The taxonomic level at which the cemented habit is distributed varies considerably from superfamily level (e.g Hippuritacea and Ostreacea), family level (e.g. Spondylidae), generic (e.g. *Myochama*) and below the species level (e.g. ecomorphs of *Chlamys pusio*). The level observed is in part related to the evolutionary longevity of the group.

3] Cementation has appeared in many totally unrelated stocks, although just over 50% do belong to the Superorder Pteriomorphia.

4] Certain taxonomic units of bivalves have repeatedly evolved the cemented habit (e.g. the Pectinidae), and these may be interpreted as being particularly well preadapted.

5] There are two forms of cementation; pallial cementation and byssal cementation. Only the Anomiacea employs the latter.

6] Apart from the pseudomonotids and possibly the terquemiids, the habit is restricted to post-Palaeozoic bivalves.

7] Cementation has evolved in both marine and freshwater environments.

8] Certain of the cemented bivalves have been highly successful over geological time (e.g. the oysters and rudists), both in terms of their ability to form 'reefs' and their high taxonomic diversity and abundance.

CHAPTER 3

THE MECHANISM OF CEMENTATION

3.1 INTRODUCTION

How do bivalves cement? In order to tackle the problem of the origins of various cementing clades we have to be able to answer this seemingly basic question. Only then are we equipped to make reasonable suggestions as to the preadaptive requirements for cementation.

Chapter One established the paucity of published information on the mechanism of bivalve cementation. The only effective investigative work has been confined to the larval cementation of oysters. The means by which adults of these, or other, taxa cement has received remarkably little attention. Although several authors, for example Morton (1974), Nicol (1978) and Yonge (1979), have speculated on the mode of adult cementation in various bivalves, their explanations have been based on theory rather than observation. An important part of this thesis has been devoted, therefore, to the study of living cementers, in an attempt to gain the information which is of vital importance to studying the evolution of the cemented habit.

This chapter has two major aims. The first is to discover the actual mechanism of cementation, and the second to pinpoint the basic adaptations which enable this mechanism to work. Chapter Four will look at these adaptations in more detail and distinguish between those which were preadaptations in ancestral taxa and those which are secondary consequences of the cemented habit. The work recorded here is concerned with the shell-cemented bivalves rather than the byssally cemented Anomiacea. Although the latter have achieved the same permanence of attachment, they have done so by an entirely different means, for which the preadaptive condition would surely have been dissimilar. In

addition, the anomiids' novel means of cementation has only evolved once in the fossil record and so does not share the interest of the multiple acquisition of the shell cemented habit. Nevertheless, members of the Anomiacea have been used in a comparative role in the study, for the interesting question remains as to why this exceptional means of attachment was exploited and what, if any, preadaptive characters might have been lacking, so preventing shell cementation.

3.2 HOW DO BIVALVES CEMENT ?

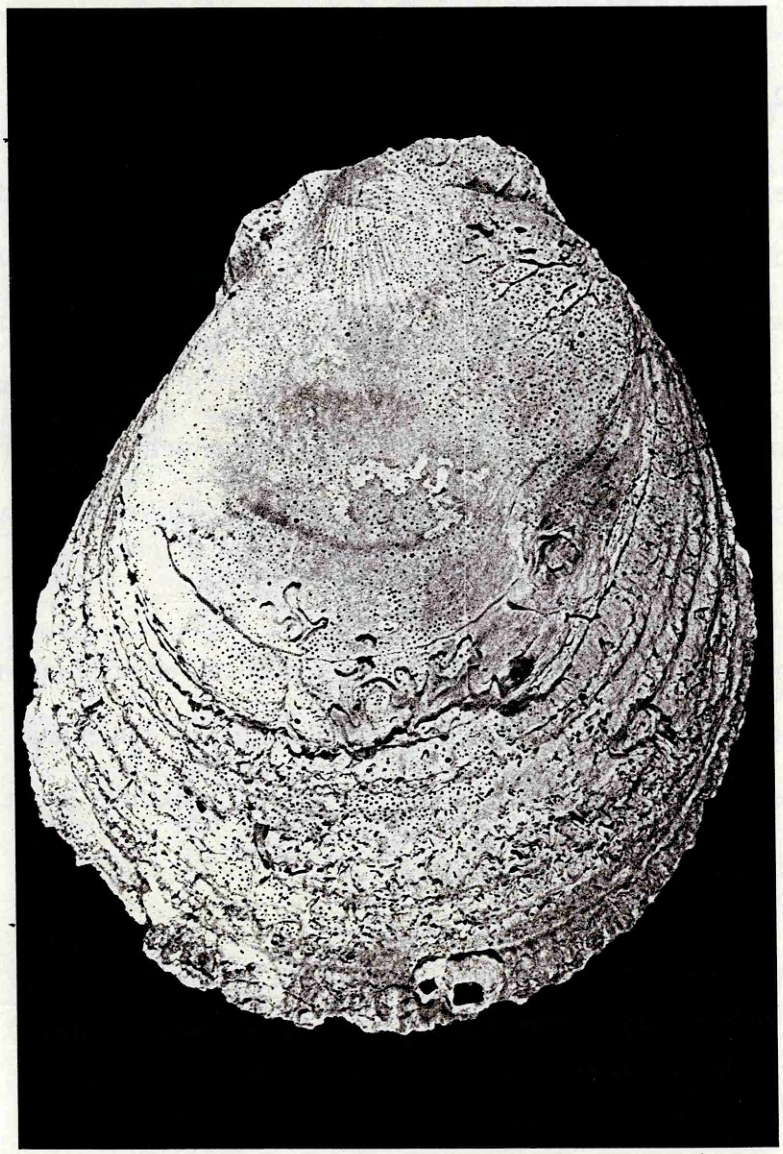


Figure 3.1 *Hinnites giganteus:* right valve detached from substratum. Valve height = 160mm.

Cementation disrupts the genetically controlled shell sculpture such that the valve conforms to an irregular substratum. Figure 3.1 shows the underside of the right valve of *Hinnites giganteus* which has been detached from the substrate. The fine pectinid ribbing of the byssally attached juvenile phase, and the somewhat coarser ribbing of the shell after 'lift off', are suspended over the portion of the valve which was cemented. Clearly the mechanism of shell cementation must be intimately related to the shell secreting process described in Section 1.3.2. In order to produce a shell which conforms closely to an irregular surface the mantle margins and periostracum must play a crucial role.

3.2.1 The principles of adhesion

De Bruyne (1962) examined how one body adheres to another, the understanding of which is necessary for this study. Two surfaces will adhere when they are brought close enough together for significant electromagnetic interaction. In practice this separation is of the order of Angströms, and de Bruyne stresses that adhesion is usually brought about through the agency of a fluid. This fluid, which may afterwards harden, flows into irregularities in the surfaces, smoothing them. This creates new boundaries close enough together to be bonded by electromagnetic forces.

These requirements must be considered in any enquiry into the mechanism of bivalve cementation. Clearly the ultimate requirement for cementation is that the 'lower' valve of the bivalve must be placed in close enough proximity to the substrate for adhesion to occur.

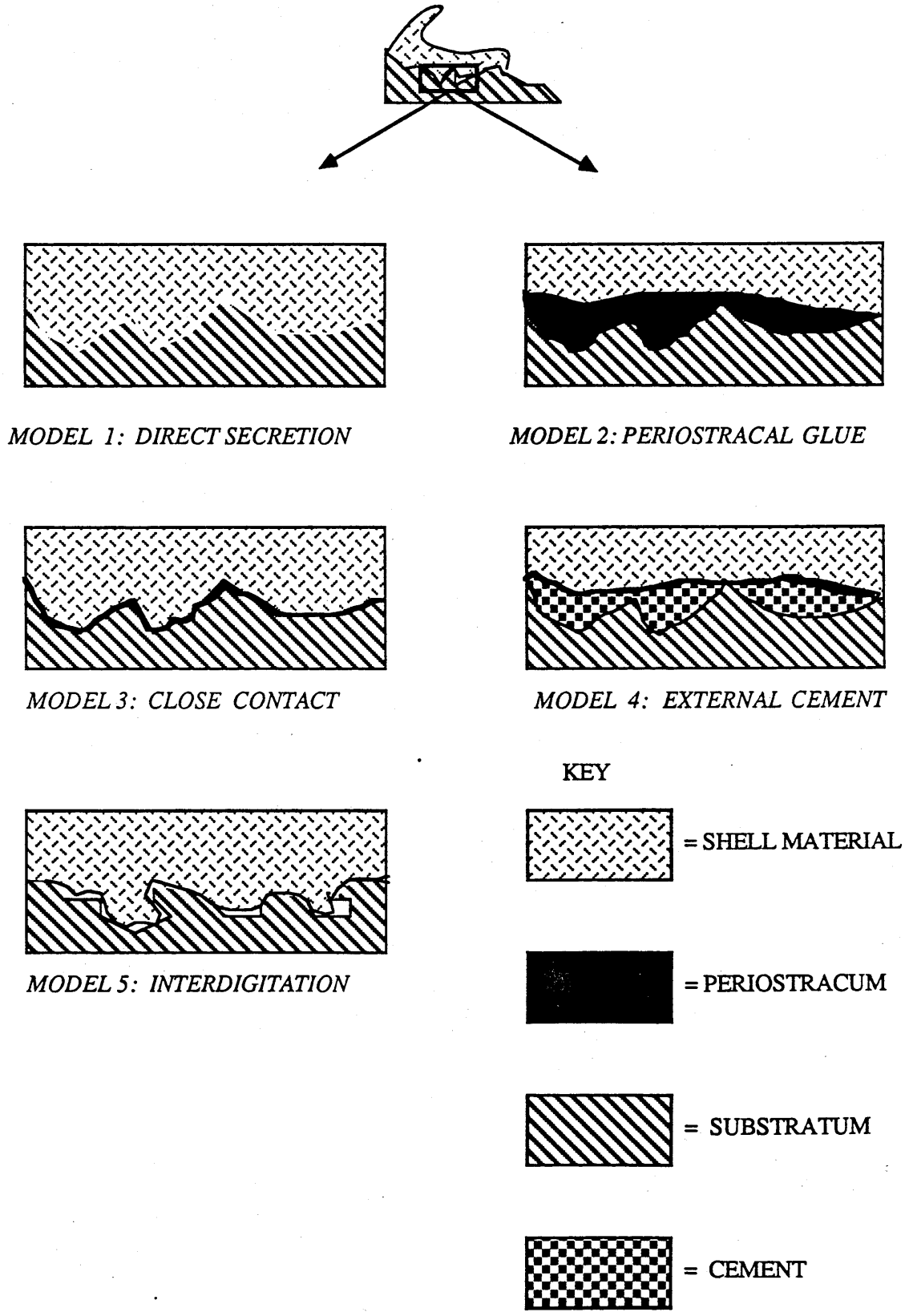


Figure 3.2: Hypothetical models for bivalve cementation. See text for explanation.

3.2.2 Possible models

Armed with the above information and a knowledge of bivalve shell formation it is possible to construct five theoretically plausible models by which bivalves might cement. These possible models are illustrated by Figure 3.2 and described below. Only by experimental testing of these could any decision be made upon their validity. Within the framework of these models it has also been possible to include the speculations of other authors; however, their inclusion here within any model is dependent upon my interpretation of the authors' reasoning.

It should be possible from each theoretical model to make certain predictions, which may be used as criteria for testing the model. Predicted implications of the models for the appearance of the mantle margins and the attachment surface are given, in Table 3.1.

Model 1 Direct secretion

Taylor, Kennedy and Hall (1969) regard the principle function of the bivalve periostracum to be the template on to which the calcareous portion of the shell forms. It is conceivable that in cases where the mantle margins are closely applied to the substratum the periostracum might be dispensed with. The attachment surface itself would then take the role of template and act as the nucleation site for the extrapallial fluid. In this instance the shell would be directly attached to the substratum.

Several authors have reported that various cementing bivalves lack a periostracum, for example the oysters (see Stenzel, 1971), *Spondylus* (Logan, 1974) and *Chama* (Vance, 1978). Such observations, if correct, would support this model.

Model 2 Periostracal glue

In this hypothetical model, the periostracum emerges not as a solid sheet but as a sticky mass which adheres to the substratum. Thus the cementation is effected by a

mucopolysaccharide 'glue'. This scenario requires very little modification to the basic mode of shell secretion, the only major change being that the periostracum does not solidify within the periostracal groove.

Many authors' views can be accommodated within this model. Yonge reiterated seven times that cementation occurs "presumably by way of the periostracum" (1960, 1962, 1967b, 1978a, 1979, 1981 and 1983). Only in 1979 did he elaborate on this while discussing attachment of *Hinnites multirugosus*, using it to explain cementation in all other dissoconchs. He suggests (p.98) " this must involve attachment of a semifluid periostracum to the substrate as well as to the outer surface of the shell. The extrapallial cavity is extended forward so that the outer fold can protrude beyond the margin of the valves..... to attach its secretion to the substrate or, more accurately, to the inner surface of the periostracum now attached to the rock". Unfortunately Yonge never tested this suggestion and his extending it to cover the mechanism for all other cementing bivalves is shown below to be unjustified.

Morton (1974), in discussing *Cleidothaerus,* supposed that the outer layer of the periostracum is "sticky", allowing the attachment. His assertion is not unreasonable when considering the Pandoracea. Yonge (1952) and Prezant (1979) both describe Lyonsiidae, also members of the Pandoracea, with unusually thick and fluid periostraca. Yonge refers to *Entodesma saxicola* which uses its "semifluid" periostracum to incorporate sand grains on to the surface of the shell. Such observations may seem to lend credence to Morton's supposition.

Model 3 Close contact

A very simple model would predict that a bivalve shell could be constructed close enough to a substrate for adhesion to be possible without a sticky periostracum. The resulting shell/substrate overgrowth is very similar to that achieved by Model 1 but differs

fundamentally in that this model involves a periostracum. To achieve adhesion in this way requires no major modification to the basic shell secreting mechanism.

There is an obvious flaw to this simple model, in that there is no fluid phase in between shell and substrate to smooth out surface irregularities to enable electromagnetic interaction.

Model 4 External cement

Model 4 is essentially an elaboration of Model 3, utilising a fluid cement between the periostracum and the substratum. There is no need yet to predict the origin of this cement; possible options include secretion by or through the periostracum, or perhaps by some other part of the anatomy, e.g. the foot. The cement may be either organic or calcareous. [The use of the term organic in this context is restricted to carbon based compounds and does not extend to calcium carbonate, although clearly this is likely to be of biogenic origin.]

This model includes the mode of cementation in the larval oyster described by Cranfield (1973a) where the shell adheres on a drop of mucopolysaccharide secreted by the foot. Nicol (1978) defines cementing bivalves as those which are attached by secretions of calcium carbonate; however he provides no evidence or explanation as to how this might be achieved.

Model 5 Interdigitation

This model does not strictly conform to the concept of adhesion, but still presents a plausible method of fixation. Spurs and flanges produced in the outer shell layer may interdigitate with irregularities in the substrate surface such that an interlocking attachment is formed, (see Figure 3.2). Bernard (1986) suggests that this may be the mechanism of attachment utilised by the idiomorphic ribbing of *Chlamys pusio*.

MODEL	PERIOSTRACUM	SHELL/SUBSTRATUM
1	Absent; mantle margins closely applied to the substratum	Shell structure directly abuts onto the substratum. Perfect fit.
2	Semifluid; variable thickness and amorphous	Outer shell layer does not closely mirror topography. Periostracum accumulates in hollows.
3	Solid layer	Perfect mirror of topography. Periostracum forms a sandwich between valve and substratum.
4	Solid layer	Cement layer clearly visible between the shell and substratum.
5	Solid layer	Very loose interdigitating contact between the substrate and shell.

TABLE 3.1 Predictions on the state of the periostracum and substrate contact indicated by each of the hypothetical models.

The models outlined above are all based on modifications of the basic mechanism of bivalve shell secretion. Each may be subject to endless minor variation. The aim of the following sections is to raise and answer pertinent questions which will, for a given bivalve, establish which of these models is most acceptable and which may be eliminated. The important point to remember is that cementation is a polyphyletic adaptation within the Bivalvia - identifying the mode of attachment in one clade does not allow us to make sweeping deductions about the mechanisms utilised in other cementing clades.

3.2.3 Is the periostracum continuously secreted during the cementation process?

Model 1 may be distinguished from the rest by its prediction that the cementing valve, at least during cementation, has no periostracum. The continuation of the periostracum below the cemented valve has not previously been demonstrated. Therefore this is one of the key questions to answer, and one which will immediately either support or eliminate the model of direct secretion.

Materials and methods

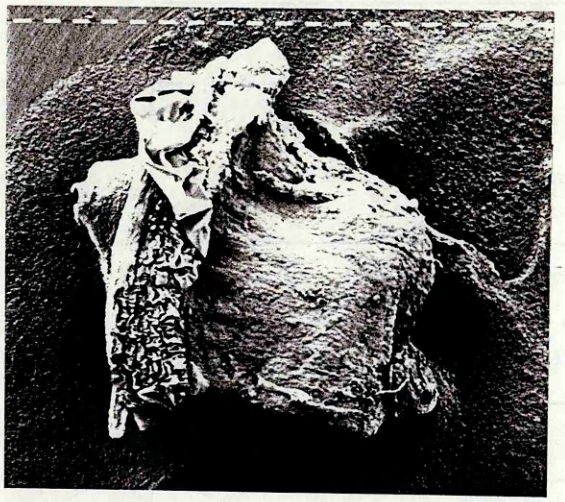
Preparations were made of the mantle margins of representatives of every living clade of cementing bivalve for investigation with SEM. Living material was available for all except the following genera; *Plicatula, Dimya, Saccostrea, Etheria, Myochama* and *Cleidothaerus,* in which instances preparations were made of specimens preserved in alcohol. Only individuals actively cementing were chosen for study; there can be little doubt that in non-attaching phases of the life history, when normal shell growth occurs, a periostracum must be secreted.

Mantle, like any other tissue, contains a large proportion of water which must be removed prior to electron microscopy. The movement of the water/air interface through an air dried tissue produces an unacceptable amount of shrinkage and distortion, therefore it is necessary to prepare material by the Critical Point Drying (CPD) technique, see Figure 3.3.

The concept of CPD was established by Anderson (1951) when he described the drying of biological specimens by immersing them in liquid carbon dioxide and then taking the ambient fluid to its Critical Point. Any fluid has a critical temperature and pressure (the Critical Point) such that the surface tension is zero and the liquid turns imperceptibly into a gas. Thus if a biological specimen is dried by taking its ambient fluid to its Critical

Point, the liquid will escape the tissue without the gross damage caused by surface tension forces associated with air drying. Water is an impractical ambient fluid (Tc =374°C, Pc =217.7 Atmospheres), therefore carbon dioxide with its lower Critical temperature 31°C and pressure 72.9 Atmospheres is used.

a)



b)

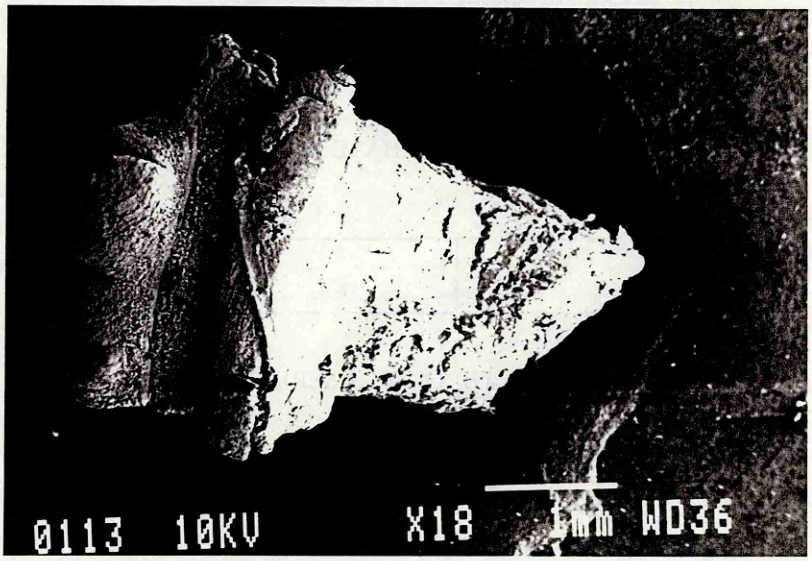


Figure 3.3: Mantle margins of *Mercenaria mercenaria* (Veneracea) dissected with identical original dimensions, (a) air dried, and (b) Critical Point Dried. Printed to same magnification.

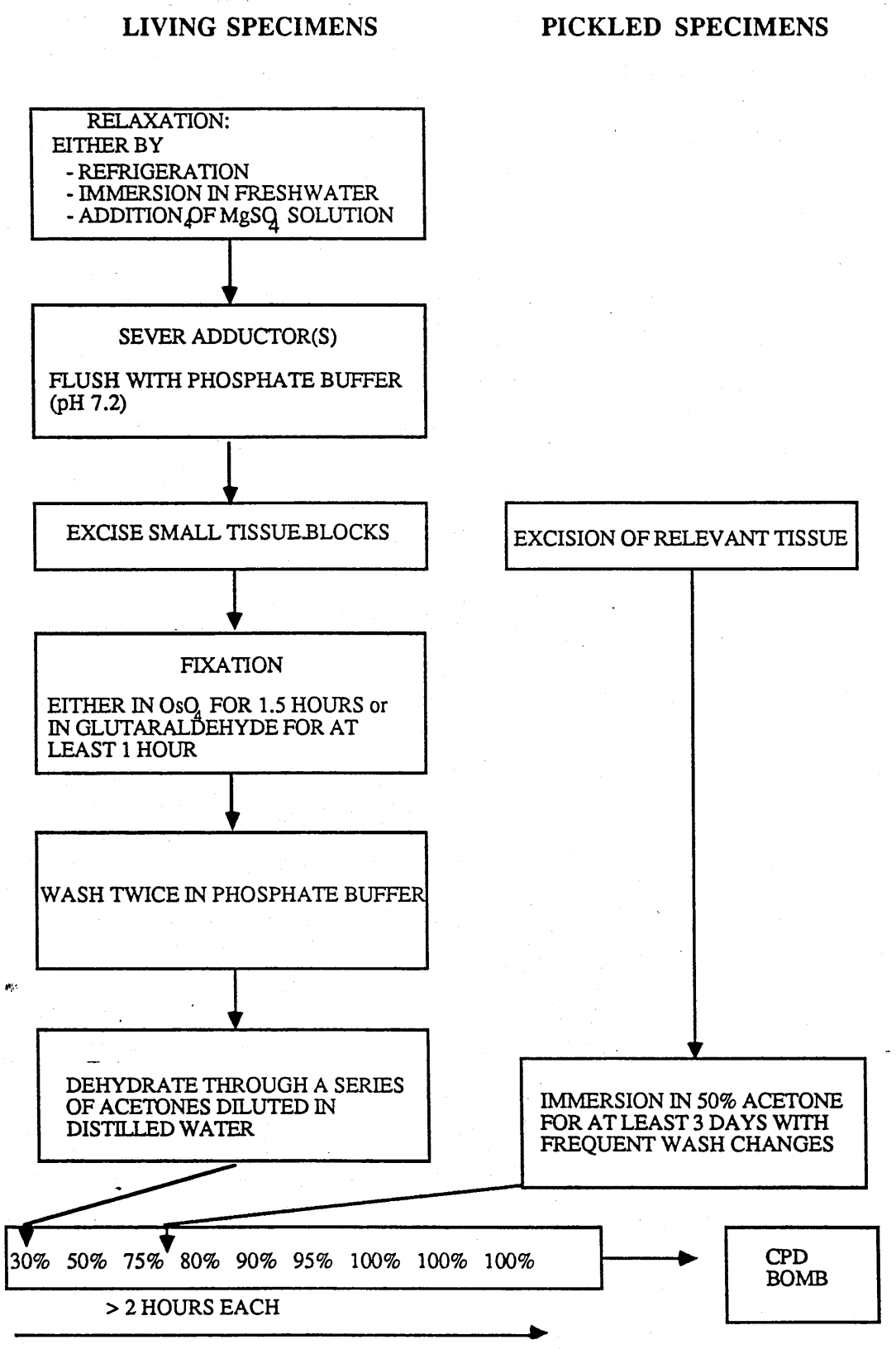


FIGURE 3.4: Methods used for the preparation of both fresh and preserved material for Critical Point Drying.

Standard preparation techniques for CPD are given by Hayat (1978), whilst Bubel (1973) gives a more specific account applied to molluscan tissue. In the course of this study it has been necessary to modify the preparation of CPD material, in order to optimise results. Figure 3.4 shows the methods used. In particular, there is no precedent in the literature for the resurrection of specimens preserved in alcohol or formaldehyde. It has been possible to achieve excellent three dimensional preparations of pickled material with good detail. For example, a specimen of *Plicatula imbricata* collected by J.D.Taylor in 1974, preserved in alcohol and prepared by the method given in Figure 3.4, provided evidence of details of the periostracum, mantle epithelium cells and cilia.

[Although the method of CPD is a familiar tool of biologists, it has as yet received little attention from palaeontologists. Yet the technique has much to offer the palaeobiologist in providing a means of looking at comparative biological material in the same form and by the same means as fossil specimens. Hill (1987) used CPD of modern sporangia for comparison with fossil examples, whilst Waller (1981) utilises the technique in investigating larval *Ostrea edulis*. In particular the technique has extraordinary potential in various taphonomic studies, see Martill and Harper (1990).]

Mantle margins preserved in this way were mounted on aluminium stubs, sputter coated with gold and investigated by SEM.

Results

All mantle margins studied were of the basic tri-lobate morphology, typical of most bivalves, see Figure 1.3. Figure 3.5 shows micrographs of all but one of the groups studied, clearly illustrating that in each there is a periostracal sheet (P) emerging between the outer mantle fold (O) and the middle mantle fold (M). The periostracum appears in most as a very fine, folded sheet, torn in dissection.

FIGURE 3.5 Illustration that members of each of the living clades of cementing bivalves possess a periostracal sheet in the attached valve during cementation. All material is critical point dried as described in the text. P=periostracum, O=outer mantle fold, M= middle mantle fold, I=inner fold and S=shell. LV and RV refer to left and right mantle lobes.

A *Ostrea edulis* LV. (EMH 0001) Galway Bay. (Bar=10μm).

B *Crassostrea angulata* LV (EMH0334) Isle of Mull.

C *Crassostrea gigas* LV (EMH0372) MAFF. (6mm=1mm)

D *Saccostrea sp.* LV (EMH0201) Pickled material from Thailand.

E *Hinnites giganteus* RV (EMH0278) Material from Canadian Fisheries.

F *Hinnites giganteus* RV (EMH 0279) Material from Canadian Fisheries.

G *Chlamys pusio* RV (EMH0216) Port Erin.

H *Spondylus gaederopus* RV (EMH0008) Boreham Wood Tropical Imports.

I *Plicatula imbricata* RV (EMH0177) ex NHZ specimen.

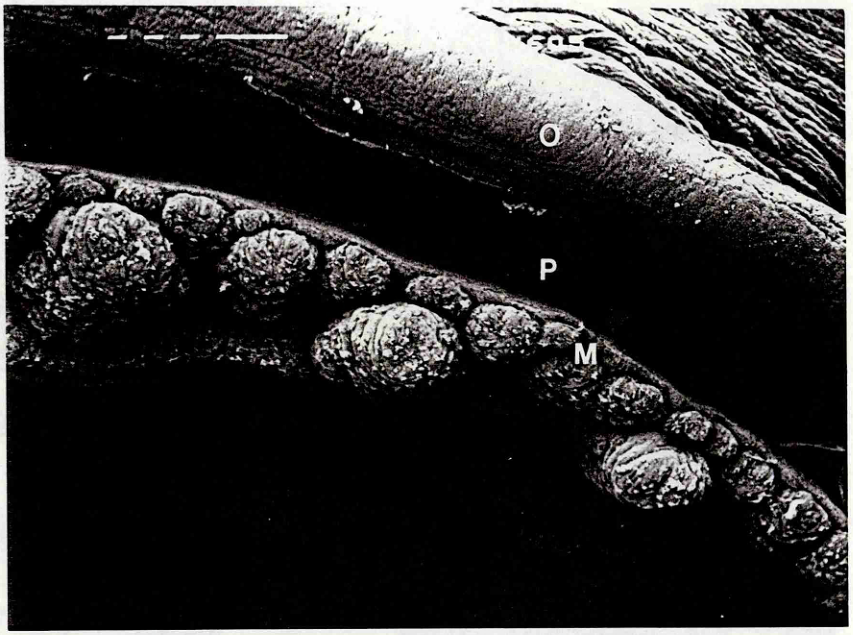
J *Etheria elliptica* LV (EMH0285) MNHN specimen.

K *'Chama' sp* RV (EMH0189) Boreham Wood Tropical Imports.

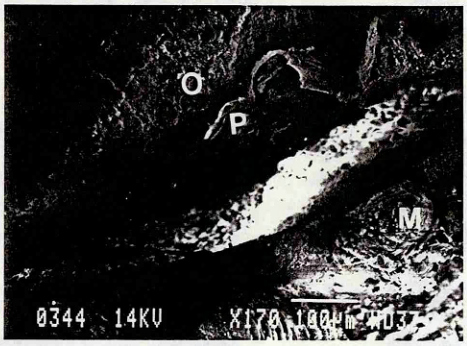
L *Cleidothaerus albidus* RV (EMH0197) New South Wales, Australia.

M *Myochama anomioides* RV (EMH0200) New South Wales, Australia.

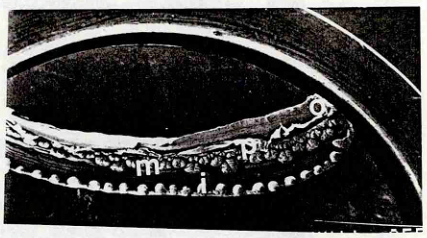
A



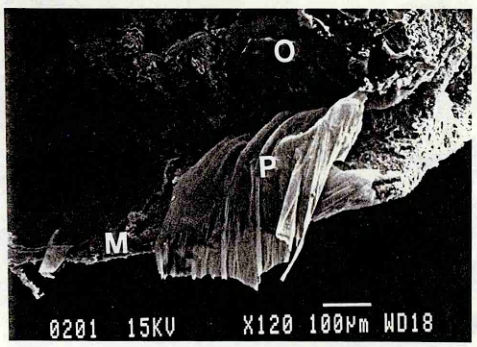
B



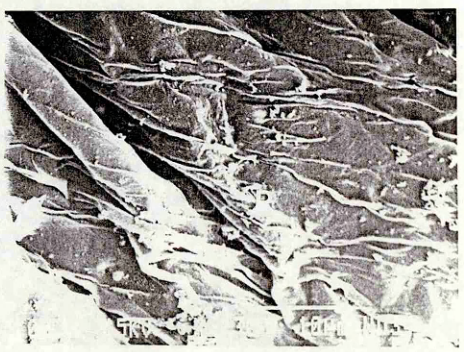
C



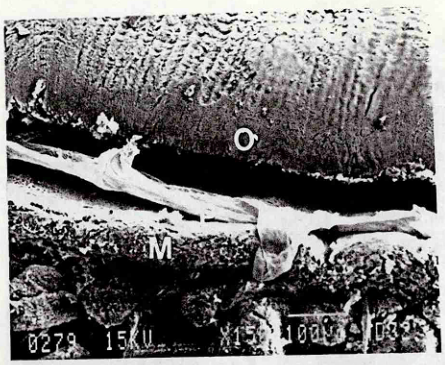
D



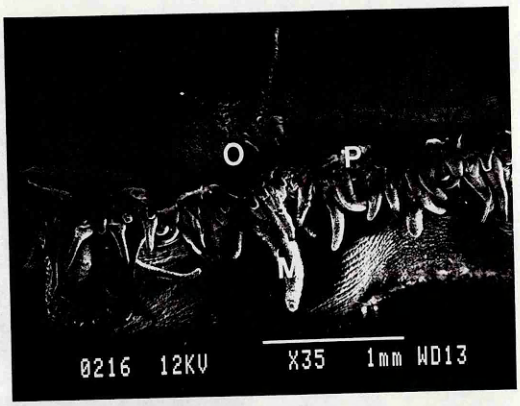
E



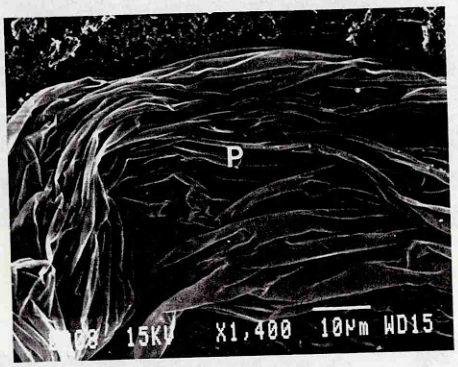
F


O
M
0279 15KV

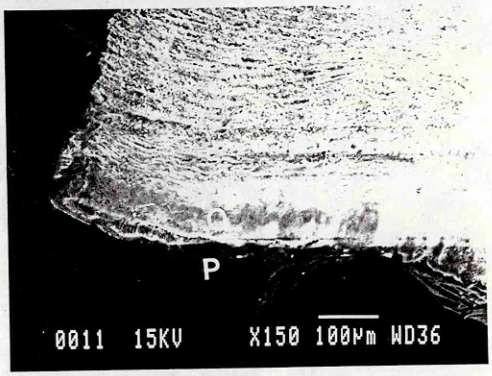
G


O
P
M
0216 12KV X35 1mm WD13

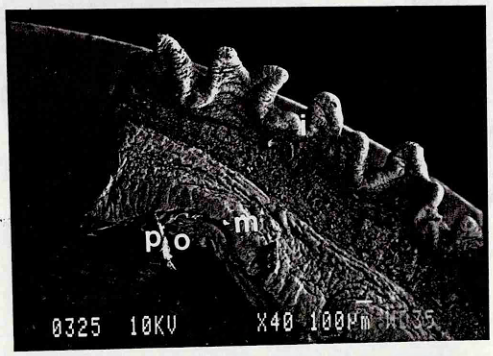
H


P
15KV X1,400 10µm WD15

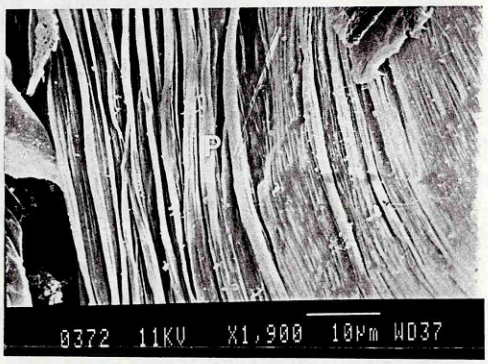
I


P
0011 15KV X150 100µm WD36

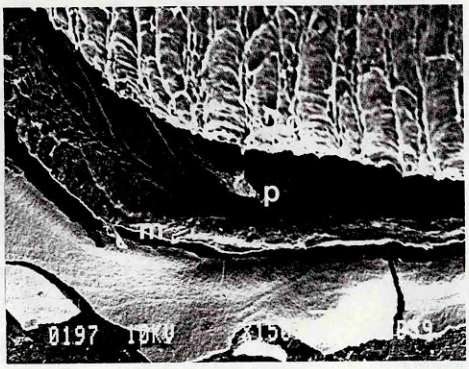
J


i
p
o
m
0325 10KV X40 100µm

K


P
0372 11KV X1,900 10µm WD37

L


p
m
0197 10KV

M


O
P

The absentee is *Dimya*. Modern Dimyidae are rare, restricted to deep water; the only material available for this study was a pickled specimen, now air dried, given by B. Morton. This specimen failed to rehydrate well enough to resolve good anatomical detail. However Yonge (1978b) refers to *Dimya corrugata* as possessing "a thin periostracal sheet". Although we are not told that this particular individual was actually cementing at the time of Yonge's observation, it is probably safe to assume that the dimyids also continuously secrete periostracum.

Reports of cementing bivalves lacking periostraca, such as Logan (1974) and Vance (1978), are thus clearly erroneous, see Figures 3.5 H and K for periostraca in *Spondylus* and *Chama*, respectively. These reports, along with those of earlier authors that oysters lack a periostracum (see Stenzel 1971), are probably founded on the fact that many of the cementing bivalves have very thin periostraca, often not discernible to the naked eye or conventional light microscopy.

It is difficult to demonstrate that the periostracum, although secreted at the mantle margins at the time of cementation, is actually present between the shell and substratum. Again this problem is probably associated with the extreme thinness of the periostracal sheet. However, it has been possible to identify with certainty the somewhat thicker periostracal sheet below the cemented valve of *Cleidothaerus albidus* (see Figure 3.6) and *Myochama anomioides* and, after etching, to reveal similar structures in *Crassostrea.*

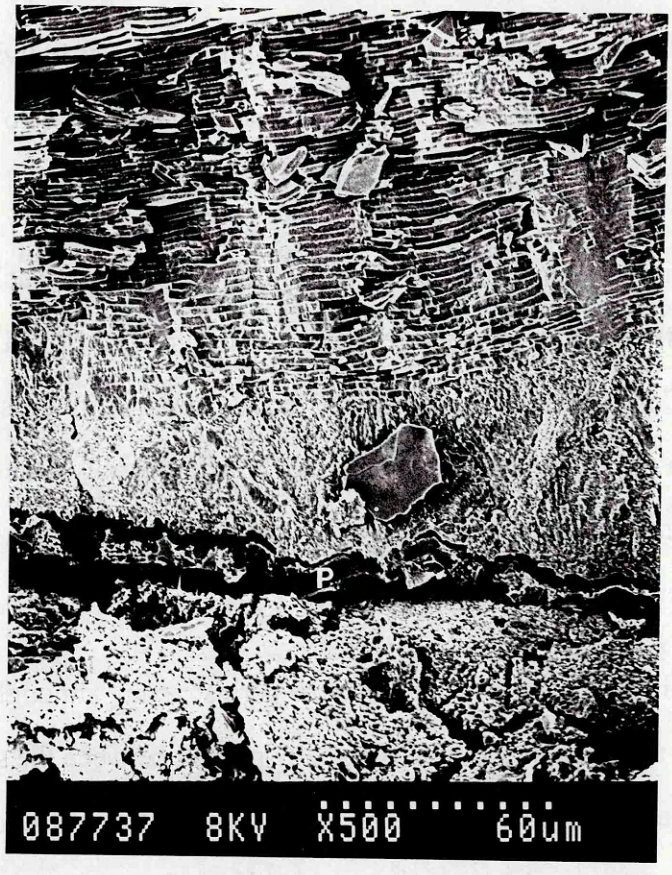


Figure 3.6: Periostracum (P) visible between the substrate and the right valve of *Cleidothaerus albidus*. Stub EMH0323. This specimen has started to spall away from the substratum during preparation.

Discussion

By demonstrating that each of the modern cementing bivalves continue to secrete a periostracum during cementation, I was able to eliminate Model 1 from the enquiry. Direct shell secretion is not the mechanism by which modern bivalves cement.

The sheet-like form of the emergent periostracum, shown in Figure 3.5, strongly suggests that the sheet is exuded as a solid rather than the fluid required to fulfil Model 2. In particular micrographs A and B tend to nullify Galtsoff's observation that the periostracum of the oyster is secreted as a "stringy fluid" (1964). However, confirmation of this is given later.

Are we able to reject Model 1 for fossil forms such as rudists or pseudomonotids? The periostracum is a fundamental part of the molluscan shell. Its principle functions lie in the provision of a site for nucleating crystallites (Taylor and Kennedy, 1969) and the isolation of the extrapallial fluid from the poisoning effects of seawater (Clark, 1976). Other authors have identified further periostracal functions, for example protection of the shell from dissolution, sealing the valve margins against water loss (Tevesz and Carter, 1980) and in anti-predatory adaptations (Wright and Francis, 1984). There are no proven cases of any modern bivalve genuinely lacking the structure, although certain internal shelled gastropods and cephalopods (*Spirula*) have been claimed to possess no periostracum (Meenaskshi and Scheer, 1970 and Mutvei, 1964). The method by which bivalves secrete their shells may be seen as part of the historical-phylogenetic constraint which controls shell morphology (see Raup 1972). Thus since the periostracum plays such a pivotal role in the process it may be supposed that in all externally shelled molluscs the periostracum will exist in some form. It is, therefore, most unlikely that any of the extinct bivalve taxa possessed no periostracum.

3.2.4 Is cementation effected by a totally organic substance, or does it have a mineralised component ?

The nature of the adhesive cement bonding the shell to the substrate may be investigated by selective removal of various components. There are two options; firstly to remove all calcareous material and secondly to remove all organic material. The former option is

undesirable as it inevitably leads to dissolution of the shell and possibly the substratum as well and also offers no opportunity of replicating observations on fossil material. Therefore a series of simple experiments were designed to remove the organic components.

Authors who support the organic glue model for cementation predict that its composition will be that of a tanned mucopolysaccharide, i.e. similar to periostracum. Carter and Aller (1975) liberated calcified periostracal spikes from their organic matrix by immersion in hypochlorite, and even the most robust insect cuticle (another tanned polysaccharide) may be dissolved in concentrated potassium hydroxide (W.A. Foster, personal communication). Therefore, if the supposition that bivalves cement using an organic glue is correct, it should be possible to break the adhesive bond by subjecting them to the above reagents.

Materials and Methods

Adherent specimens of two and six week old individuals of *Crassostrea gigas*, and adults of *Ostrea edulis, Lopha cristagalli, Saccostrea* sp., *Myochama anomioides, Spondylus hystrix, S. gaederopus, Chama* sp., *Chlamys pusio, Etheria elliptica* and *Cleidothaerus albidus* were placed in either concentrated bleach or KOH, boiling for the first two hours. A simulation of an organically attached bivalve was used as a control. The artificial bivalve was created by glueing a lump of epoxy resin onto shells of *Modiolus modiolus* with intact periostraca, see Figure 3.7.

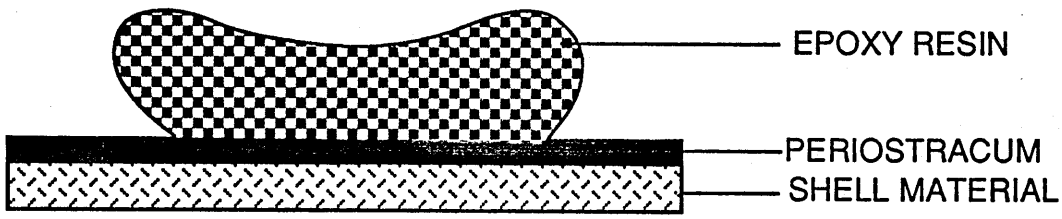


Figure 3.7 Simulation of an organically cemented bivalve. The epoxy resin acts as an artificial bivalve attached to a shell substrate by the periostracum of the *Modiolus*. Removal of the periostracum allows sundering of the 'bivalve' from its substratum.

Results

Within fourteen days, the two week old spat of *Crassostrea gigas* had sundered from their substrates (both glass and calcite). All specimens of *Chama, Myochama* and *Etheria* had separated within twelve weeks, after which the separated portions were investigated under SEM. There was no observed separation in any of the other bivalves treated, even after 24 months. The control experiments resulted in the periostracal layer dissolving very rapidly (<4 weeks) resulting in the breaking of the bond between the epoxy resin mass and its substrate (the shell of the *Modiolus*).

Discussion

The results of the very simple control experiment illustrate that it is possible for a bivalve which is attached to its substrate merely by an organic glue to be separated by removing the organic material in the manner described. The majority of adult cemented bivalves tested in this way did not detach, even after 24 months of trial and hence provide evidence that attachment is not solely organic. Of those individuals that did detach, *Myochama* and *Etheria* had been attached to an organic substrate, the periostraca of *Eucrassatella* and conspecifics, respectively. In both these cases the separation can be attributed to dissolution of the substrate rather than the bond; Figure 3.8 shows the underside of the right valve of *Myochama* dissociated in this way. The periostracum is clearly intact, despite prolonged bleaching, indicating calcification.

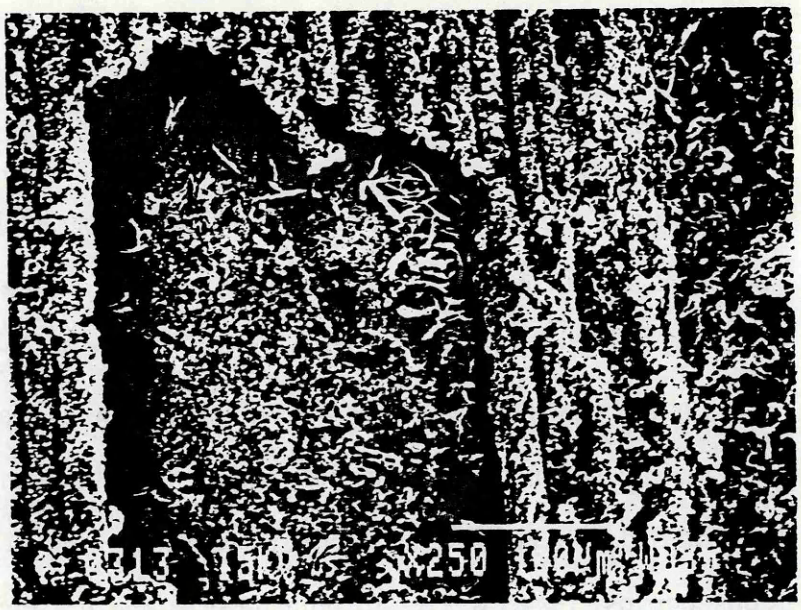


Figure 3.8: Periostracum from the underside of the attached (right) valve of *Myochama anomioides*. Despite prolonged immersion in KOH the periostracal sheet remains intact, apart from having sustained mechanical damage during preparation. Stub EMH0313.

The separation of both *Chama* and the youngest oyster spat from *inorganic* substrata provides evidence that these are truly organically attached. The case of the latter contrasts sharply against the behaviour of the six week old spat which did not detach. From this it is possible to infer that the switch from the organic cementation described by Cranfield

(1973a, 1974) and Tomaszewski (1981) to a calcareous cement occurs between two and six weeks after initial settlement.

Further evidence that the cement of adults of a majority of cementing bivalves is mineralised is given by elemental analysis, and is described in 3.3.2.3.

The findings of the above experiment are very instructive. Apart from Nicol's (1978) assertion that cementation was achieved by a calcareous secretion, there have been no other supporters for a mineralised cement. Biologists are preoccupied with decalcification; most investigators of adherent organisms, for example Tomaszewski (1981) for oysters and Soule (1973) for bryozoans, remove all calcareous matter from their subjects prior to study. It could therefore be suggested that the lack of published information in support of calcified attachment is due to a differing experimental approach.

The results of this experiment alone do not disprove any of the models postulated in 3.2.2, although it does add the stipulation that the periostracal glue invoked in Model 2 must be calcified, and rules out the option that in Model 4, the external cement may be organic.

The conclusion that most cement is mineralised should not be unduly surprising. The apparent ease by which cementing bivalves fossilise attached to their substrata strongly suggests that the mode of cementation is not affected by post mortem degradation, as does the observation that in trying to part individuals from their substrata it is the shell rather than the bond that tends to fail.

3.3 DETAILED EXAMINATION OF THE BOND

The above two sections have illustrated that all cementing bivalves possess a periostracum and that the attachment to the substratum contains a mineralised component. These findings prompted a series of more detailed investigations into the nature of that

periostracum, in particular compared to non-cementing bivalves, and the precise relationship between the shell and substratum.

3.3.1 The periostracum

Despite its ubiquity, the bivalve periostracum is often neglected in the literature. Apart from detailed accounts of its formation in *Mytilus edulis* (Dunachie, 1963) and *Anodonta* (Bubel, 1976), and a generalised review by Saleuddin and Pettit (1983), the periostracum has figured little in malacological literature unless it is conspicuously 'odd', for example the shaggy periostraca of certain Arcacea. Vague pronouncements may be made. For example, when describing periostracal thickness terms such as 'thick', 'thin' and 'excessively thin' are used (e.g. Tebble, 1966), but with no agreed conventions to indicate what dimensions apply to any of these descriptions, they are essentially useless.

It has therefore proved necessary to initiate a thorough investigation as to the nature of various periostraca.

3.3.1.1 Thickness: a comparative survey of cementing and non-cementing bivalves

Materials

Along with representatives of all the living clades of cementing bivalves, periostraca have also been obtained from a large number of non-cementers belonging to a wide range of taxonomic groupings and autecological categories. Material was collected for this study in Dunstaffnage Bay (Oban), Galway Bay and the Isle of Arran, supplemented by live specimens from Millport Specimen Supplies and preserved specimens from the NHZ.

Methods

All material was prepared in the manner described in section 3.2.3. In order to measure periostracal thickness it was necessary to select a common point at which measurements

could be made. Saleuddin and Pettit (1983) describe three phases of periostracum; (i) *Forming* - where the periostracum is travelling down the groove and the thickness is increasing progressively with further secretion, (ii) *Free* - where the sheet extends from the mantle margins to the shell, and (iii) *Outer* - where the periostracum is exposed on the outer surface of the shell. Obviously the outer periostracum is subject to thickness diminution by physical and biotic abrasion (e.g. the rasping of grazing gastropods), and bacterial and fungal decay, whilst the forming periostracum is progressively increasing in thickness. This requires that the thickness measurements used in this study should be made from the free periostracum, where it emerges from the periostracal groove, or very rarely from outer periostracum when it is adjudged to be intact.

In all pleurothetic bivalves, periostracum was measured from the 'lower' valve. Since in the vast majority of cases this was the periostracum of the right mantle lobe, it was the dextral periostracum which was measured in orthothetic taxa.

Measurements were derived in three ways;

(i) *Direct measurement*

Prepared mantle margins were mounted in the SEM such that the fractured edge of the periostracum was held perpendicular to the lens. Alternatively, undamaged periostraca were isolated from shell material and mounted vertically in slotted microscope stubs. In this way it was possible to take micrographs of the edge of a periostracal sheet, from which the thickness could be determined. This technique is only suitable for the more rigid periostraca which do not curl over or vibrate in the vacuum chamber.

(ii) λ *measurement*

For the less rigid periostraca it was necessary to devise a new method of determining thickness, based on the folding properties of the sheet. Consider a thin sheet of infinite flexibility, which may be folded into tight isoclinal folds whose wavelength (λ) is related

to the thickness (T) of the sheet. The theoretical lowest value for λ obtainable will be 2T. However, in practice the measured value for λ will be larger than 2T, as flexibility of the periostracal sheet needs to be accounted for, i.e. $T<\lambda/2$. Nevertheless, an acceptable estimate of T may be gained by making multiple measurements from each sample.

(iii) *From the literature*

In only a very few cases do authors supply periostracal dimensions (e.g. Morton, 1974), but others have published micrographs from which it is possible to derive measurements by either of the above methods.

Measuring periostracal thickness is fraught with problems; certain species e.g. *Arca* have periostracum which splits easily into laminar sheets, making the true thickness difficult to measure. Also to what extent is the parameter subject to intraspecific variation? This latter point is of great importance. It was not always possible to measure more than one or two specimens and so how meaningful are the results?

In order to investigate the intraspecific variation in periostracal thickness, measurements were taken from 20 specimens of *Mytilus edulis*. A mean value of 66µm was established, with a standard deviation (σn-1) of 12.5µm. This would seem to imply that even within this relatively thick periostracum the variation is not that great, < 20% of the mean value. In fact the variation may not be so great; the thicker values are obtained from areas of the periostracum close to the ligament. Although a systematic investigation has not been carried out for other taxa I have observed no evidence to suggest that periostracal thickness is not relatively constant in a species. This would seem to indicate that the use of a series of measurements from a single animal will suffice.

TABLE 3.2: Periostracal thickness (μm) estimates for a range of living bivalves. Details given of taxonomic position and life habits. Bu=burrowing, By=byssate, Bo=boring, F=free and C=cemented. Stub details are given in Appendix 1.

Superfamily	Species	Life habit	Thickness μm	Stubs used
Nuculacea	*Nucula nitida*	Bu	2.5	368
Solemyacea	*Solemya parkinsoni*	Bu	100	Beedham and Owen (1965)
Arcacea	*Anadara erthraensis*	Bu	57	BM stubs
Arcacea	*Arca tetragona*	By	>100	323
Arcacea	*Arca tortuosa*	By	17	BM stubs
Arcacea	*Barbatia obliqua*	By	200	BM stubs
Arcacea	*Glycymeris glycymeris*	Bu	50	168,207
Arcacea	*Glycymeris kepelliana*	Bu	50	BM stubs
Mytilacea	*Aulacomya magellicanus*	By	156	BM stubs
Mytilacea	*Geukensia demissa*	By	71	BM stubs
Mytilacea	*Lithophaga lithophaga*	Bo	73	BM stubs
Mytilacea	*Lithophaga nigra*	Bo	30	BM stubs
Mytilacea	*Modiolus adriatica*	By	64	BM stubs
Mytilacea	*Modiolus barbatus*	By	29	BM stubs
Mytilacea	*Modiolus modiolus*	By	107	60,122, 142, 184
Mytilacea	*Modiolus tulipa*	By	22	BM stubs
Mytilacea	*Musculus impactus*	By	72	BM stubs
Mytilacea	*Musculus nigra*	By	54	BM stubs
Mytilacea	*Mytilus californianus*	By	124	BM stubs
Mytilacea	*Mytilus edulis*	By	66	e.g. 119,136,183
Mytilacea	*Mytilus smaragdinus*	By	50	BM stubs
Mytilacea	*Perna perna*	By	280	BM stubs
Mytilacea	*Perna viridis*	By	77	126
Mytilacea	*Septifer bilocularis*	By	66	BM stubs
Mytilacea	*Stavelia torta*	By	360	BM stubs
Pectinacea	*Chlamys pusio*	C	<1	30,55,56
Pectinacea	*Chlamys opercularis*	F	<10	70,71,181
Pectinacea	*Chlamys varia*	By	<1	38,77

Pectinacea	*Hinnites giganteus*	C	<0.5	270,271,272
Pectinacea	*Pecten maximus*	F	<0.5	144
Pectinacea	*Pseudamussium septem radiata*	F	<0.5	366
Pectinacea	*Spondylus gaederopus*	C	<0.5	158,159
Pectinacea	*Limaria hians*	F	<0.5	373
Plicatulacea	*Plicatula imbricata*	C	<0.5	166
Anomiacea	*Monia squama*	By/C	10	134,135
Ostreacea	*Crassostrea angulata*	C	<0.5	164,180
Ostreacea	*Crassostrea gigas*	C	<0.5	34
Ostreacea	*Crassostrea virginica*	C	<0.5	Carriker et al (1980)
Ostreacea	*Ostrea edulis*	C	<0.5	62,65,187
Ostreacea	*Saccostrea sp.*	C	<0.5	201
Unionacea	*Unio littoralis*	By	26	418
Unionacea	*Margaritifera sp.*	By	20	Taylor et al (1969a)
Unionacea	*Etheria elliptica* - Attached	C	0.6	282, 286
Unionacea	*Etheria elliptica* - Unattached	C	48	326
Trigoniacea	*Neotrigonia* sp.	Bu	12	Taylor et al (1969)
Chamacea	*Chama sp.*	C	2.5	188,189
Astartacea	*Astarte elliptica*	Bu	30	170,363
Astartacea	*Astarte sulcata*	Bu	12	378
Crassatellacea	*Eucrassatella kingicola*	Bu	40	312
Cardiacea	*Acanthocardium aculeatum*	Bu	1	371
Cardiacea	*Cerastoderma edule*	Bu	63	182,196
Cardiacea	*Laevicardium crassum*	Bu	36	74
Solenacea	*Ensis arcuata*	Bu	82	72
Solenacea	*Ensis ensis*	Bu	92	49
Tellinacea	*Gari fervensis*	Bu	166	365
Tellinacea	*Pharus legumen*	Bu	28	BM stubs
Arcticaea	*Arctica islandica*	Bu	117	72,167
Corbulacea	*Corbula gibba*	Bu	143	381,401
Veneracea	*Macrocallista sp.*	Bu	20	BM stubs
Veneracea	*Venerupis sp.*	Bu	3	174,209
Veneracea	*Venus casina*	Bu	2	BM stubs
Myacea	*Mya arenaria*	Bu	50	379,383
Myacea	*Mya truncata*	Bu	48	BM stubs
Hiatellacea	*Hiatella arctica*	Bo	22	417,74,377
Pandoracea	*Cleidothaerus albidus*	C	7	197,198
Pandoracea	*Cleidothaerus maorianus*	C	10	Morton (1974)

Pandoracea	*Myochama anomioides*	C	13.6	199, 200

Analysis

Table 3.2 shows that periostracal thickness varies widely within the class, from a mere fraction of a micron in the oysters and scallops, to 360μm for the mytilid *Stavelia torta.*

For the purposes of this thesis arbitrary limits to the descriptive terms thin and thick has been set at 20μm. Ultrathin describes those periostraca of less that 1μm.

It would appear that various taxonomic groupings have similar periostracal thicknesses. For example, all measured members of the Pectinacea had ultrathin periostraca, whereas the Mytilacea and the Arcacea, although displaying a tremendous range of thickness, can all be described as thick. Clark (1976) regards thick periostracal sheets as a primitive bivalve character. Intuitively, therefore, it would seem that there is some selective advantage, in certain circumstances, to the derived state.

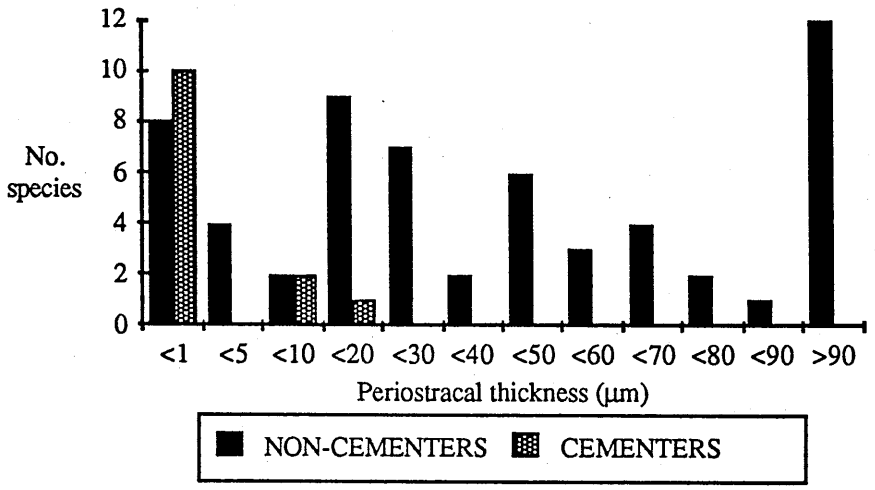


FIGURE 3.9: Histogram to show the relative numbers of species displaying periostraca of given thicknesses, for non-cementing and cementing bivalves.

Does periostracal thickness relate to life habit? A histogram, Figure 3.9, plots the numbers of recorded species in each thickness category for non-cementing and cementing bivalves. This plot can give no real indication of the absolute distribution of periostracal thicknesses within the Bivalvia; the sample size is too small and biased by multiple measurements of certain groups. It does, however, indicate the range of thicknesses observed in the class. The important point is the comparison of the data derived from cementing bivalves with that of the non-cementers. The cementing clades all possess very thin periostraca, the vast majority of which are considerably less than 1μm thick. Even the larger values recorded, all within the pandoracean cementers, are thin, the maximum being *Myochama anomioides* at 13μm. In common with other members of the Unionacea, the etheriids possess a thick (c.50μm), dark periostracal layer on non-attached valves. However, the measurements of periostracum secreted at the time of cementation reveal a value of 0.6μm, in line with those of other cementing bivalves. In addition, Gregoire (1974), remarked upon a thinning of the periostracum below the attachment scar. It would therefore seem that the thinning of unionacean periostracum in *Etheria* may be linked to the attachment process. Although, as stated previously, this study has been unable to provide data on the periostracum of members of the Dimyidae, it is likely that it too will be of minimal thickness, as Yonge refers to it as "thin". Likewise measurements were not obtainable for the extant gryphaeids. However, of all the oyster periostraca, Stenzel (1971) chose to single out that of *Hyotissa* as being particularly "poorly developed". It therefore seems likely that the Gryphaeidae share ultrathin periostraca with the Ostreidae. There may be one exception to the ultrathin oyster periostraca. Stenzel (1971) refers to that of *Striostrea* as "very strongly developed". Observations at the NHZ have confirmed that the outer surfaces of the valves of *Striostrea* are covered in a thick organic film. Without recourse, however, to living or preserved material the question as to whether this layer is genuinely periostracal or a modification of the conchiolin scales, is equivocal.

The advantage of a thin periostracum to a cementing bivalve is intuitively obvious. Consider, by analogy, the relative degree of success in attempting to wrap sheets of tissue paper and cardboard over a surface with irregular topography. In a bivalve, the thinner the periostracal sheet the more accurately it can mimic the attachment surface. Indeed, no periostracum can follow an irregularity whose radius of curvature is less than twice its own thickness.

Although there is a wide range of thicknesses recorded for byssate taxa (*Chlamys varia* <1μm; *Stavelia torta* 360μm) there is a tendency for the sheet to be thick. This observation may be largely artefactual due to the large number of Arcacea and Mytilacea measured here. Nevertheless, a number of possible advantages accrue to byssate taxa possessing a thick, spongy periostracum, such as deterrence and inhibition of boring predators, and the effective sealing of both the valve margins and the vulnerable byssal gape from the leakage of metabolite cues which may attract predators, or in intertidal forms may lead to desiccation. Burrowing taxa have a wide range of periostracal thickness (e.g. *Acanthocardia echinata* 1μm; *Eucrassatella kingicola* 40μm and *Corbula gibba* 143μm). This suggests is that the periostracal thickness displayed in each case is the legacy of the phylogenetic group to which the species belongs rather than a specific adaptation to the life habit exploited.

There are insufficient numbers of species measured for the remaining ecological categories, and therefore it is not possible to conclude that, for example the periostraca of borers is always thick, or whether the results achieved for *Lithophaga* and *Hiatella* are merely a consequence of their membership of taxa with generally thick periostraca. Only two swimming species were measured, *Chlamys opercularis* and *Limaria hians*; the ultrathin values noted are clearly in agreement with other non-swimming members of the Pectinidae, but may have, as Moore and Trueman (1971) point out, an adaptive significance in the reduction of drag.

3.3.1.2 The character of the cementing periostracum

Observations made at the mantle margins have shown that the periostracum of the cementing valve is secreted as a solid sheet of uniform thickness. The sheet is frequently highly convoluted: this may be adaptive in allowing the deep retraction of the mantle margins whilst maintaining the continuity of the periostracum, and hence of shell secretion, or may be merely a consequence of the difficulty of holding a very thin film taut.

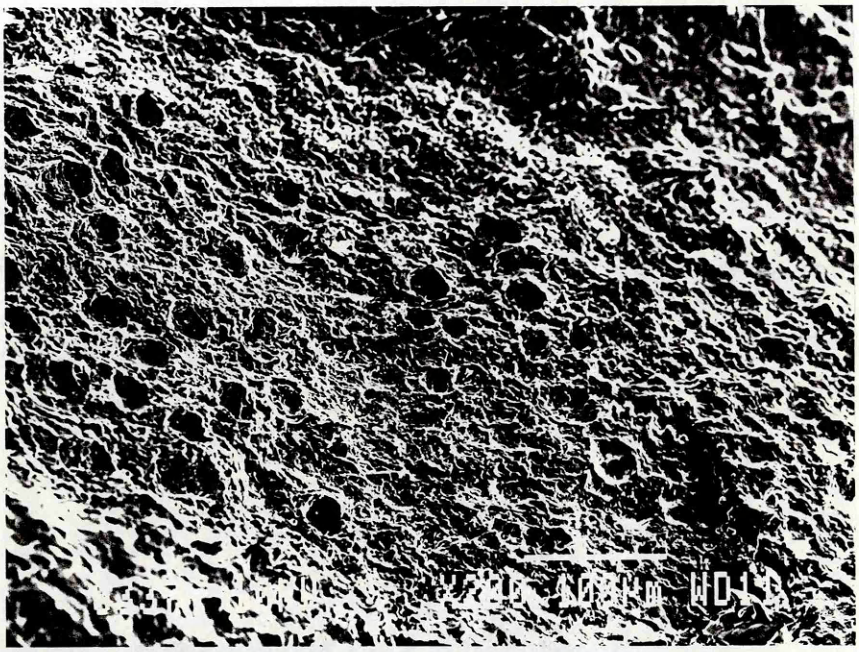
With the exception of *Etheria, Myochama* and *Cleidothaerus* most of the periostraca studied lacked any surface features discernible with SEM. Apart from the TEM work published by Cranfield (1973a) and Tomaszewski (1981) demonstrating the tripartite layering of periostraca of oysters, there are no reports of periostracal structure or ornamentation of cementing bivalves.

Those genera from which it has been possible to discern structural detail are those with the more substantial periostraca. Detailed study of these has been possible by isolating the periostracal sheet from between a calcareous substratum and the shell of the cemented valve, by gentle removal of the calcareous matter with 5% formic acid, followed by CPD. (These methods were not successful in the preparation of other thinner periostraca, as these were inevitably torn and destroyed in preparation.)

(i) *Cleidothaerus albidus*

The outer surface of the periostracum below the attachment scar of *Cleidothaerus albidus* is characterised by densely packed pores, approximately 10μm in diameter, see Figure 3.10. In cross section these pores appear dumb-bell shaped, flaring at both outside boundaries.

a)



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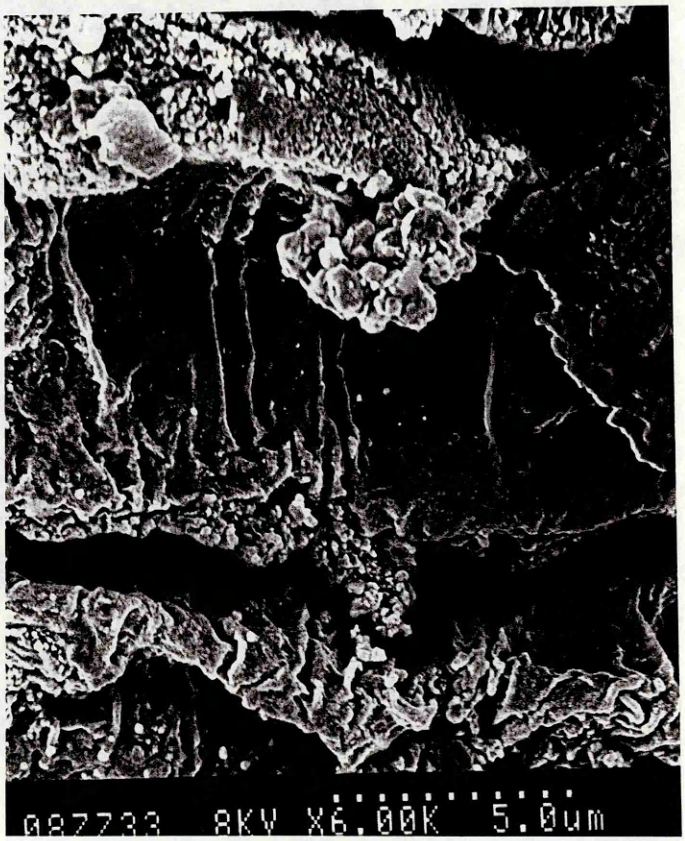


Figure 3.10: Periostracal pores in the periostracum of the attached right valve of *Cleidothaerus albidus*, prepared by decalcification. Stub EMH0337. (a) plan view of outer surface, and (b) fracture through sheet.

(ii) *Myochama anomioides*

The outer surface of the attaching periostracum of *Myochama* has a 'ropey' appearance at high magnifications. Fractured sections reveal fine (<1μm in diameter) sinuous vertical channels (see Figure 3.11). However, I have found no expression of these channels on the outer surfaces of the sheet.

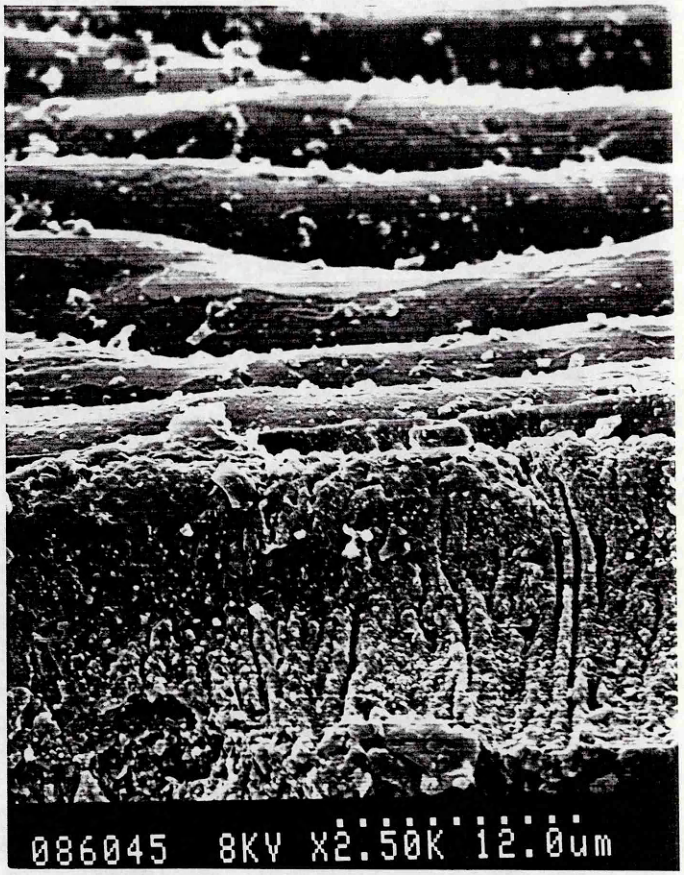


Figure 3.11: Sinuous channels through the periostracum of *Myochama anomioides*, decalcified. Stub EMH0313.

Carter and Aller (1975) describe the ubiquitous presence of calcified spicules within the periostraca of anomalodesmatans. The possibility exists that the features illustrated for *Cleidothaerus* and *Myochama* may be the voids left after the decalcification of the spicules rather than pores or channels. However, my investigations show that these pores are smaller than the spicule size reported by Carter and Aller, and are morphologically different, being elongate rather than conical. It should also be noted that the sinuous channels in the periostracum of *Myochama anomioides* are also discernible in Figure 3.17, where the specimen has not been decalcified.

(iii) *Etheria elliptica*

As stated by Gregoire (1974), the periostracum of *Etheria elliptica* is multilayered. My own preparations of decalcified material shows that the individual layers are intensely folded and only very loosely associated. I have not been able to repeat Gregoire's observations that the individual sheets are "sieve-like meshes" which contain "scattered crystals of various shapes"; however, his excellent figures support his words.

3.3.2 Investigation of the contact zone

Natural material is an unsuitable starting point for investigating the shell/substrate relationships of cementing bivalves. The problems arise from recognition of the contact zone from the substrate which may be heterogenous, extensively bored and encrusted by other epibionts. Therefore initial work was carried out on oysters deliberately grown on specific substrates, before proceeding onto specimens which were attached to more usual substrates.

3.3.2.1 Attachment to glass of *Crassostrea gigas*

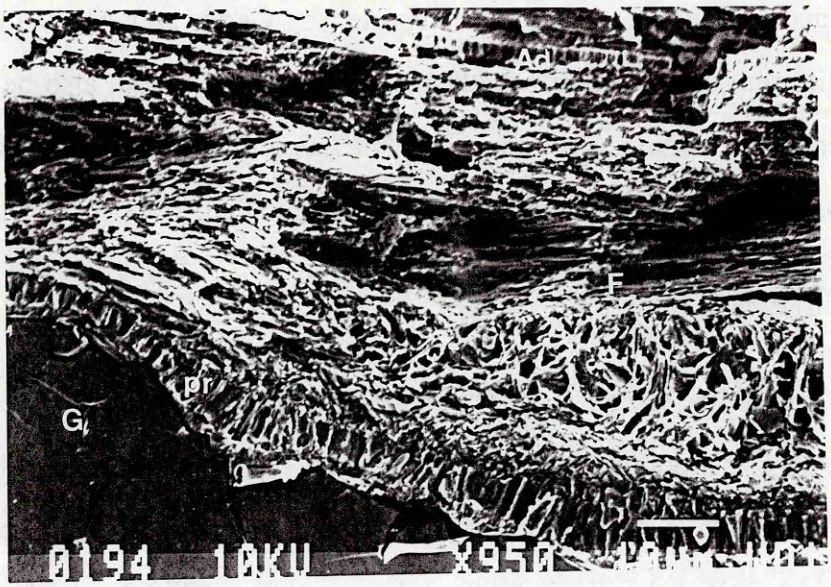


FIGURE 3.12: Six week old spat of *Crassostrea gigas* attached to a glass plate. Fractured preparation. Stub EMH0194. Pr=prismatic layer, F=foliated layer, C=chalky deposit, G=glass and Ad=adductor myostracum.

Larvae of the Pacific oyster, *Crassostrea gigas* were spatted onto ground glass plates, at the MAFF laboratories at Conwy. The glass is a readily identifiable substrate distinguishable from the shell microstructure of the oyster, whilst the exclusion of other epibionts from the settling tanks avoids confusion between cement and extraneous material.

Work commenced on the oysters six weeks after initial settlement, when the shell height attained reached 3-6mm. It has already been established in section 3.2.4 that at this age

cementation is effected by a calcified cement and that the periostracum is continuously secreted.

Material was prepared in a number of ways for inspection by SEM;

(i) Fracturing and CPD

(ii) Fracturing and subsequent removal of organic material by immersion in KOH

(iii) Untreated fractured surface

Observations

Figure 3.12 reveals the general appearance of *C. gigas* attached to the glass. The glass substratum is readily identified with its smooth uniform appearance, displaying conchoidal fracture patterns. It should however be noted that in some of the illustrated sections, the top roughened surface of the glass has a different texture, appearing as a darker band about 1μm thick, in some micrographs. Presumably this is due to some structural transformation during grinding, and is apparent in sections of glass which have not been encrusted.

The microstructure of the oyster is essentially identical to that described by Carriker, Palmer and Prezant (1980) for the congeneric *C. virginica.* The valve is bounded by a thin (5-10μm) prismatic layer, the remainder being principally composed of foliated calcite, punctuated by patches of the chalky material similar to that described in *Ostrea edulis* by Korringa (1951). A thin (c.2μm) band of adductor myostracum runs through the foliaceous layers, indicating migration of the adductor.

Even at the low magnifications of Figure 3.12 it is possible to note the way in which the oyster adheres to the glass. There is clear evidence of a cement material between the outer prisms and the substrate, although it is difficult to determine the positioning of the periostracum. It is evident that, to a certain extent, the outer shell layer does follow the

topography, although there is a definite pooling of the cement material in hollows in the substrate.

Fractures of over fifty individuals were examined in detail to elucidate the nature of the cement. Of these eleven (EMHOO52, EMH0194, EMH0232, EMH0241, EMH0250, EMH0251, EMH0292, EMH0341, EMH0397, EMH0398, and EMHO399) are considered most instructive for reference.

The features and textures observed, and described below, fall into three main groups. It must be emphasised that a given oyster will not exemplify a single case but will display most, if not all, of these features and that the division is merely for the purpose of description.

(i) *Prisms next to glass*

Figure 3.13 shows an individual where the prisms of the outer shell layer seem to abut directly onto the glass substrate. There is no cement layer visible, nor is the periostracum readily perceived. This could be taken as evidence to support Model 1 where the shell material is secreted directly onto the substrate, although the model has already been discounted in section 3.2.3. Further evidence that there is a periostracum present is available where the valve passes over sharp angular notches in the substrate, for example that labelled (N) in the figure. The prismatic layer does not follow the notch but arches over it leaving a void beneath. In this preparation where the organic material has *not* been removed, the vestiges of the periostracal sheet are visible spalling from the underside of the prisms. In this instance the periostracum has formed a hammock spanning the notch rather than following the exact configuration of the substratum.

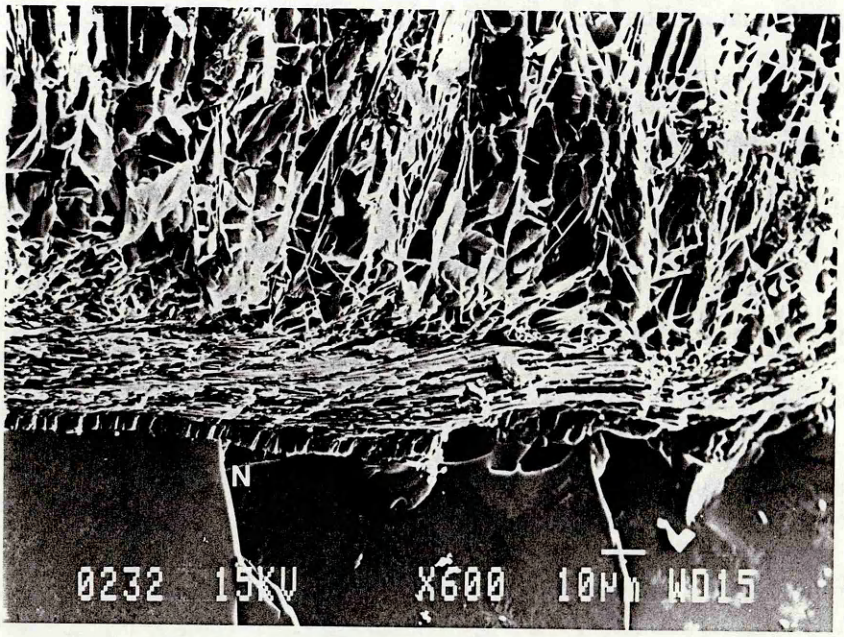


Figure 3.13: Prisms against the glass. Stub EMH0232. N= notch in the glass caused during grinding.

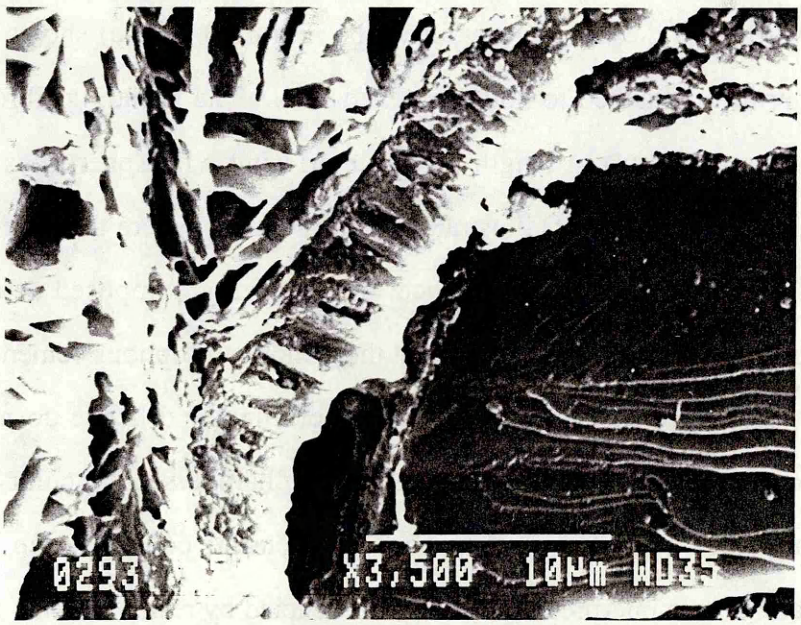


Figure 3.14: Pillars outside the prismatic shell layer. Stub EMH0293.

(ii) *Pillars*

Figure 3.14 displays the contact between the outer prisms and the substratum, where the organic material has been carefully removed. Although the prisms are in close proximity to the glass, they are separated by small, <1μm wide and 1μm high, hourglass shaped pillars. These pillars are regularly spaced and intimately related to the prisms. The gaps between the pillars are believed to be caused by the removal of the organic material and may be interpreted as representing the periostracum. The possibility that the pillars and gaps are caused by preparation artefacts or borings is rejected on the grounds of their regularity and constancy of position.

(iii) *Cavity fill cement*

In the vast majority of cases the fractured surfaces revealed a crystalline cement between the prisms and the substrate. Closer inspection of the material, Figure 3.15 (a-g), reveals that it has a fabric similar to the diagenetic cavity infill cements observed in carbonate rocks, for example see Bathurst's (1975) figures 300 and 301.

The cement occludes the space between the shell and substrate by nucleating and growing inward from the bounding void walls. Figure 3.15(a-c) shows the growth of radiating spherulites attached to both glass and shell. The radiating fibres of the spherulite may reach up to 4 μm in length before interfering with spherulites growing from adjacent walls. Figure 3.15(e-f) illustrate fracture sections where the observed cement fabric lacks the classic cavity fill appearance, instead being composed of a mosaic of equant and subequant crystals. It is likely that these more amorphous cements are fractures which do not pass through the centre of the spherulites, and hence do not display the radiating fibres. Certain fractures display empty chambers of circular cross section, <5μm in diameter. These frequently contain bacterial colonies, see Figure 3.15(a). These chambers are interpreted as the space occupied by residual fluid.

Figure 3.15: Cavity fill cement textures from fractured preparations. Pr=prisms, G=glass, c=cement, v=void and B=bacteria.

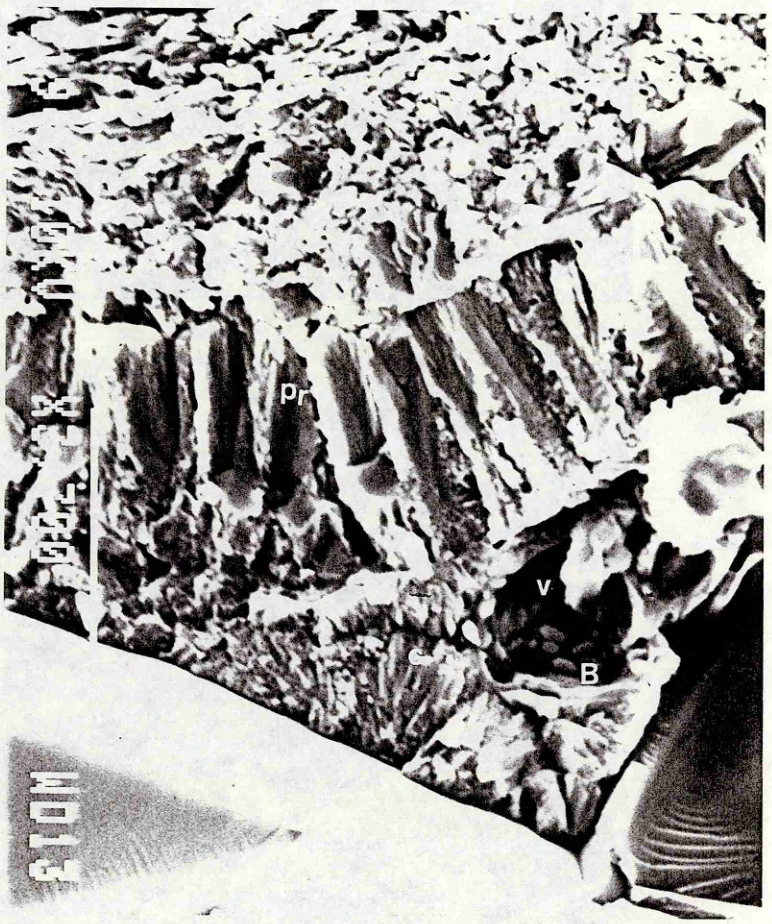
a-c) Cement spherulites growing between oyster and glass. Stub EMH0194.

d) Occlusion of an angular notch in the glass. Note growth lines in prisms. Stub EMH0194.

e-f) Cement displaying non-spherulitic form. This appearance may result from fractures which do not pass directly through the centres of spherules. Stub EMH0292.

g) Range of cement fabrics apparent under a small area of prisms. Note possible syntaxial growth of prisms in the cement. Stub EMH0194.

a)



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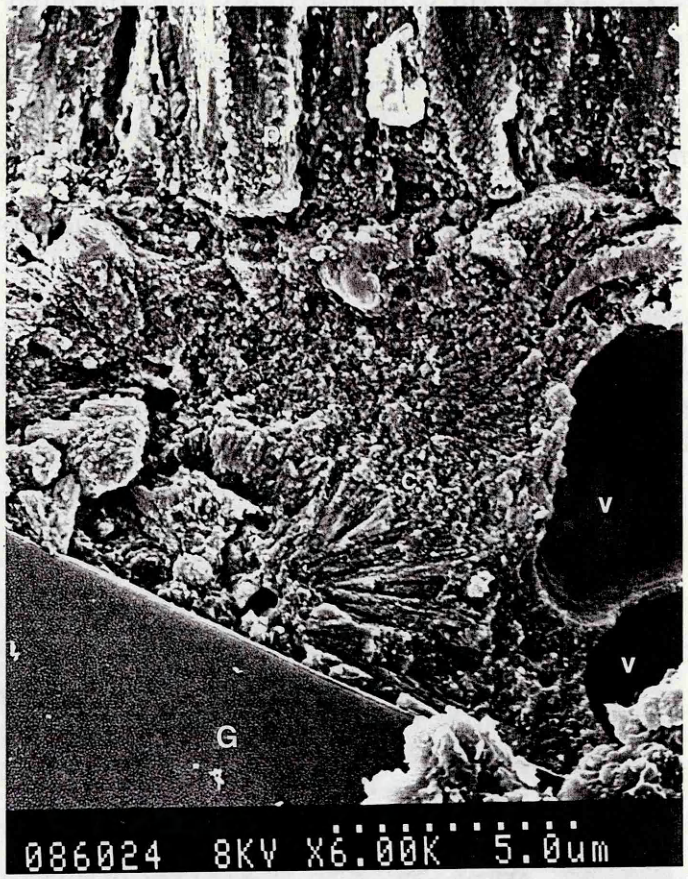

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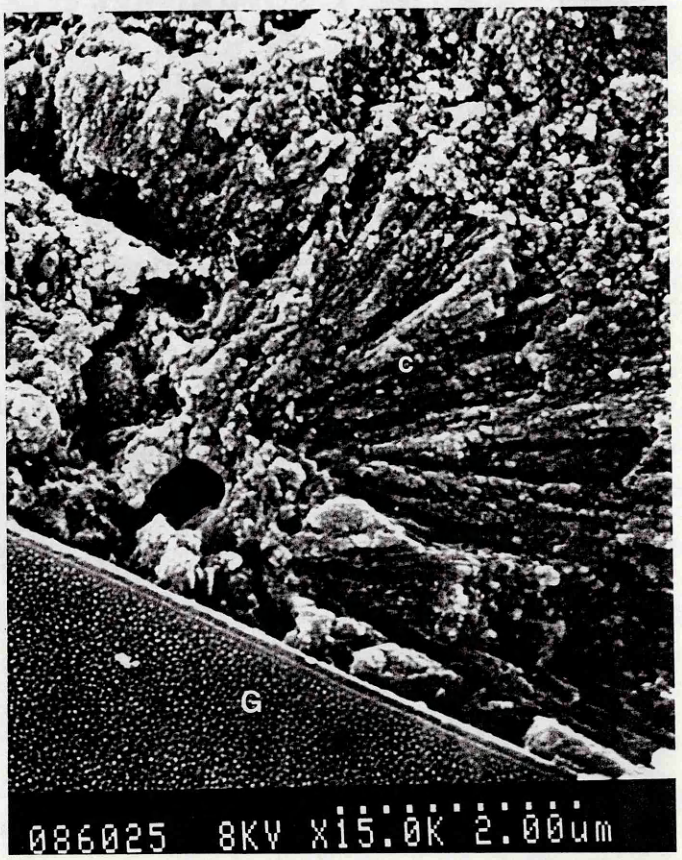
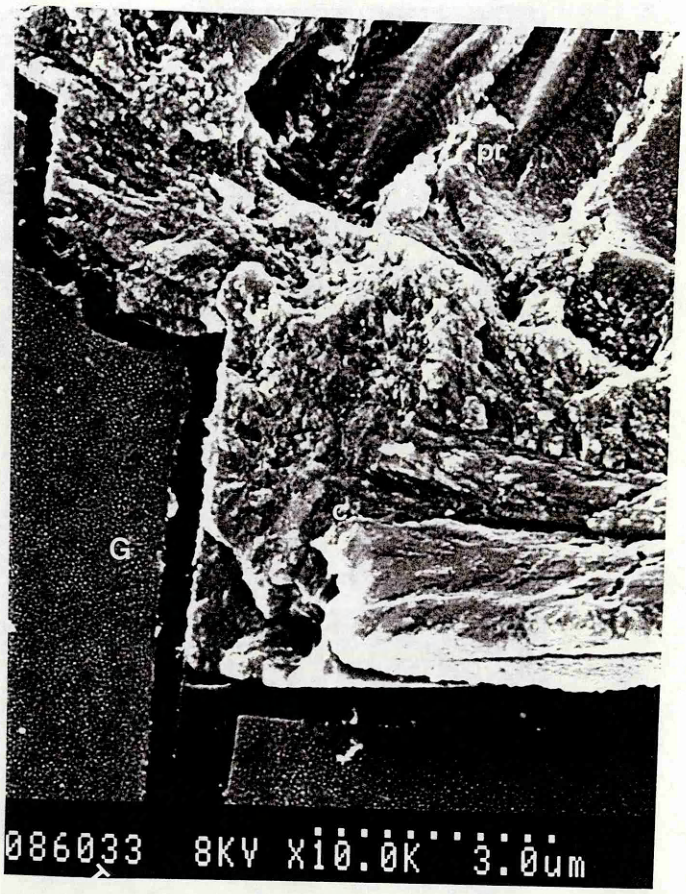


d)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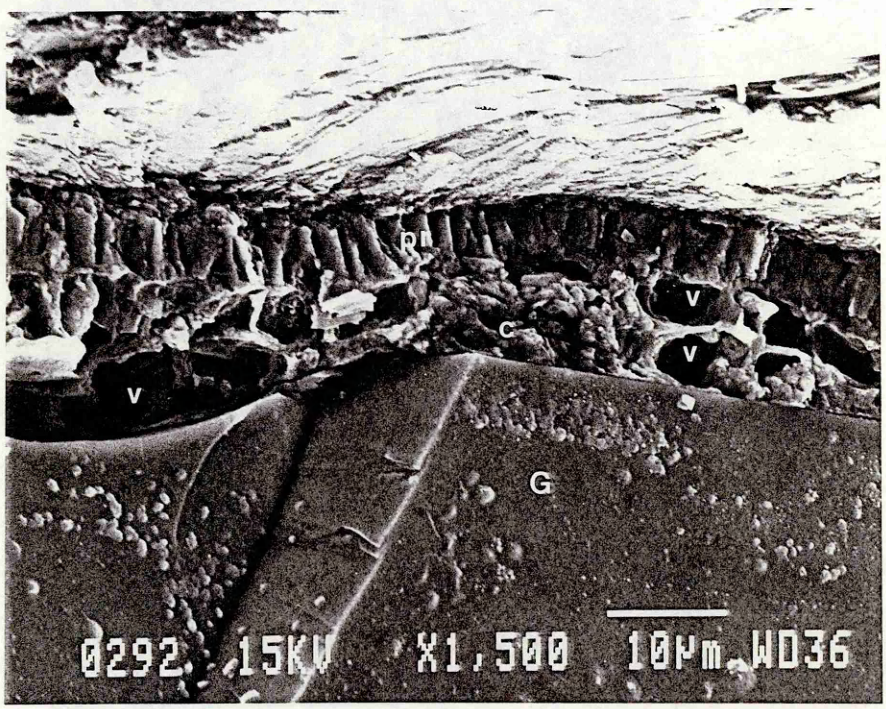
G
C
086033 8KV X10.0K 3.0um

e)


PC
V
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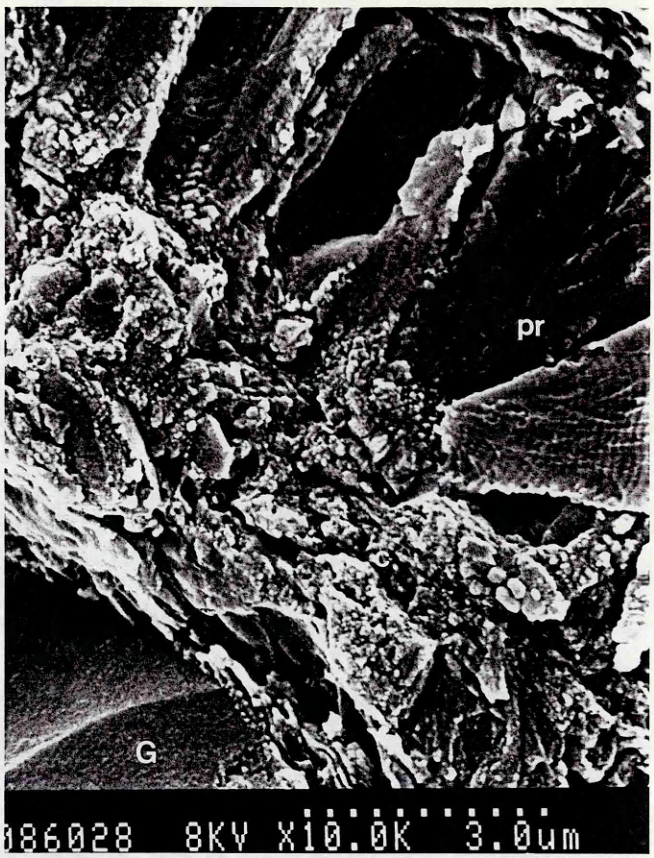
V
G
0292 15KV X1,500 10µm WD36

f)



g)

a)

b)

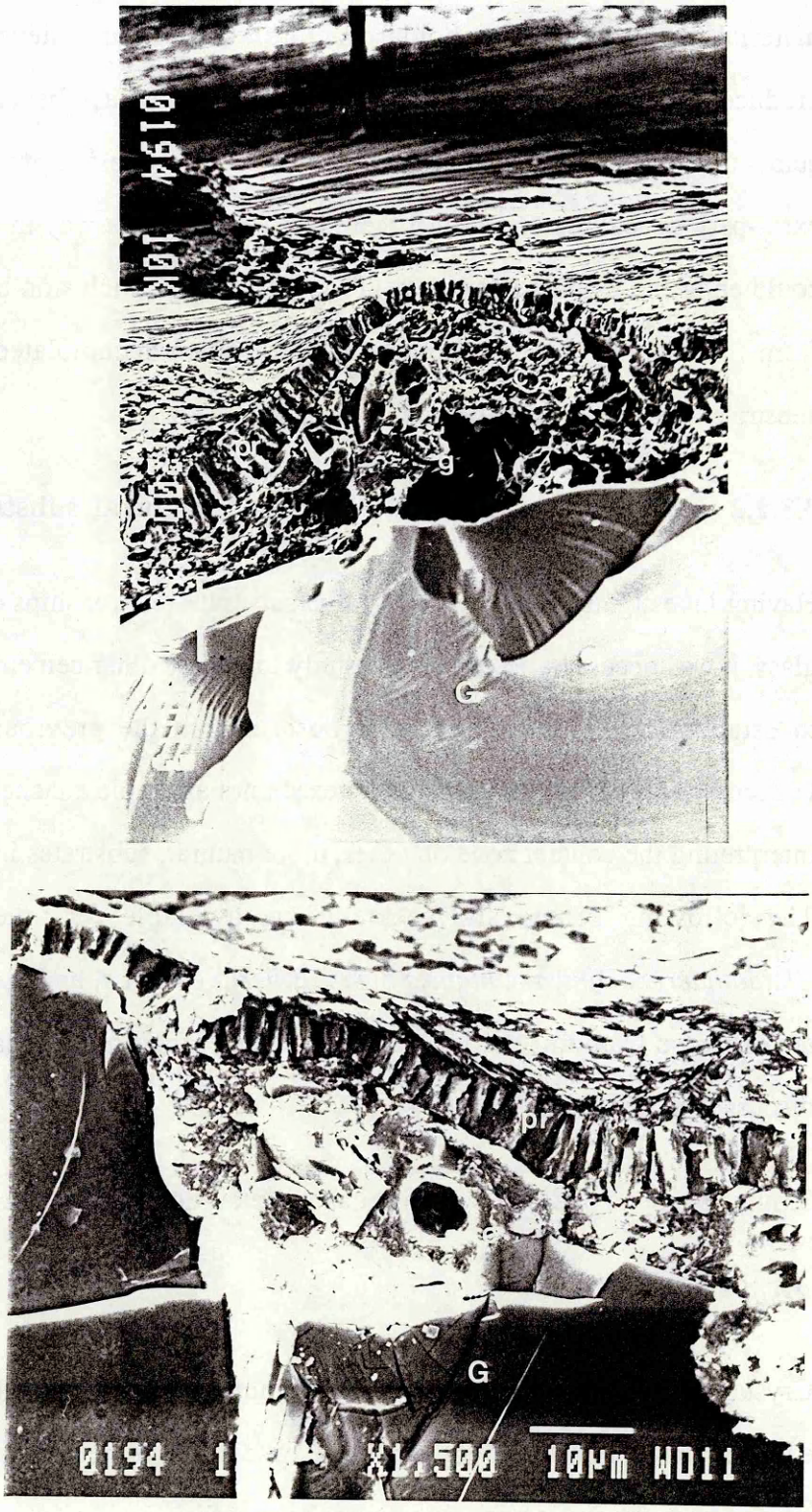


Figure 3.16: Glass shards (g) incorporated in the cement zone between shell and substratum. This feature provides conclusive evidence that the growth of this cavity fill material is extra-periostracal. Stub EMH0194.

Figure 3.16 (a-b) show areas of amorphous cement which contain particles of foreign material, displaying a conchoidal fracture. These are believed to be shards of glass produced in preparation of the spatting plates, which have become incorporated into the cement. Their presence in the cement provides conclusive proof that the cement is an extra-periostracal feature. Since there is no conceivable way in which these glass shards could enter the extrapallial cavity of the oyster, their inclusion in the cement must result from their having been entrapped in fluid which accumulated between the shell and substrate and which subsequently crystallised.

3.3.2.2 Other cementing taxa and more natural substrates

Having investigated the pattern of valve/substrate relationships of *Crassostrea* grown on glass, it was necessary to extend the study to survey other cementing bivalve taxa in order to establish whether those fabrics described in the previous section are universal. Unfortunately, other cementing bivalves are not available attached to glass, and the task of interpreting the contact zone on other, more natural, substrates is infinitely more difficult. The following genera and species were available for investigation; *Myochama, Cleidothaerus, Dimya, Chlamys pusio, Etheria elliptica,* and *Spondylus*. The Chamacea are excluded from this section on the grounds of their more organic attachment, which is discussed in Section 3.5.

Similar methods of study were used as those outlined in Section 3.3.2.1.

Results

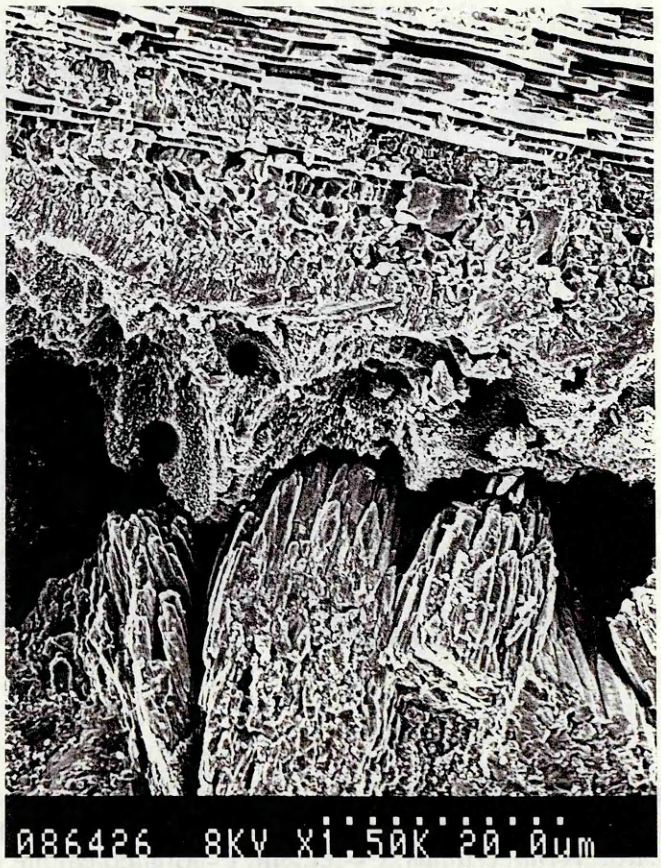
Crystalline cements between the periostracum and the substratum have been identified in each of the genera studied. In most cases this cement was amorphous rather than appearing as the fine cavity-fill textures seen earlier.

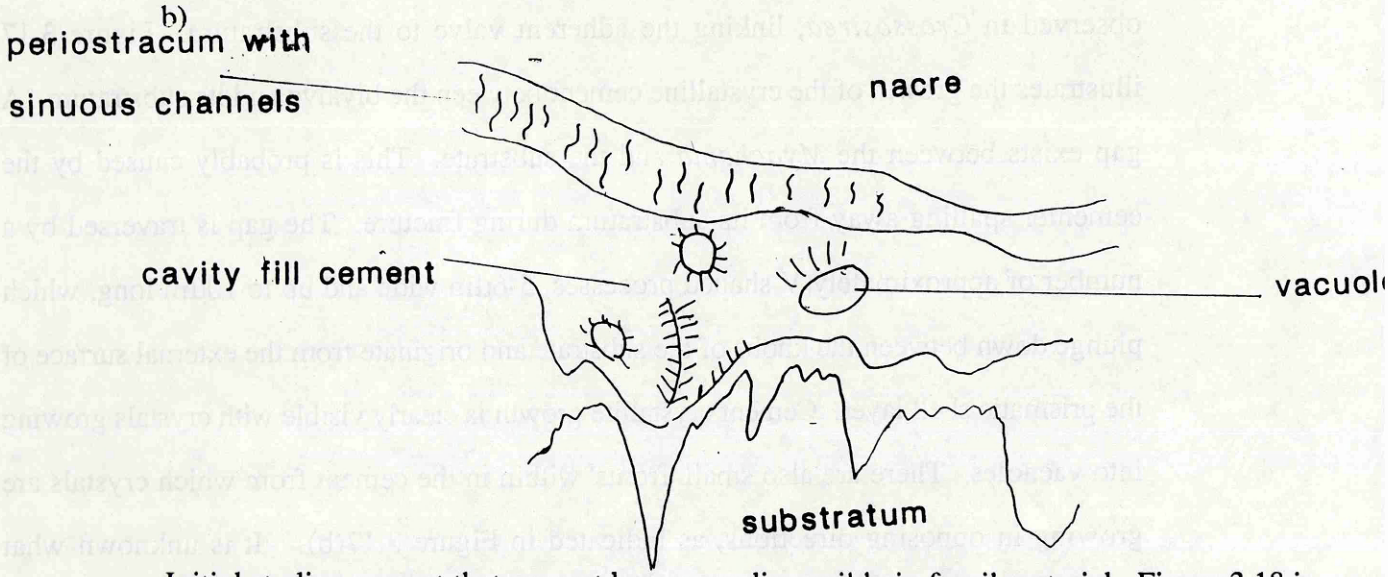
Of most interest was the attachment of *Myochama anomioides,* cemented to the shaggy periostracum of the arc *Glycymeris keppeliana*, (stubs EMH0199, EMH0237, and

EMH0246). These specimens show a numbers of struts, perhaps analogous to the pillars observed in *Crassostrea*, linking the adherent valve to the substratum. Figure 3.17 illustrates the growth of the crystalline cement between the bivalve and its substratum. A gap exists between the *Myochama* and the substrate. This is probably caused by the cementer spalling away from its substratum during fracture. The gap is traversed by a number of approximately V shaped processes, 5-6μm wide and up to 10μm long, which plunge down between the knobs of the substrate and originate from the external surface of the prismatic shell layer. Cement crystallite growth is clearly visible with crystals growing into vacuoles. There are also small 'fronts' within in the cement from which crystals are growing in opposing directions, as indicated in Figure 3.17(b). It is unknown what causes these fronts, but it is possible that they may result from mucus stringers within the extrapallial fluid.

Figure 3.17 *Myochama anomioides* attached to the periostracum of *Glycymeris keppeliana*. . Stub EMH0245. (a) micrograph, (b) interpretation.

a)





Initial studies suggest that cement layers are discernible in fossil material. Figure 3.18 is an electron micrograph of a fracture through a Gault *Atreta* attached to a fragment of inoceramid shell. In this instance there appears to be syntaxial growth of the cement onto the prisms of the *Inoceramus*.

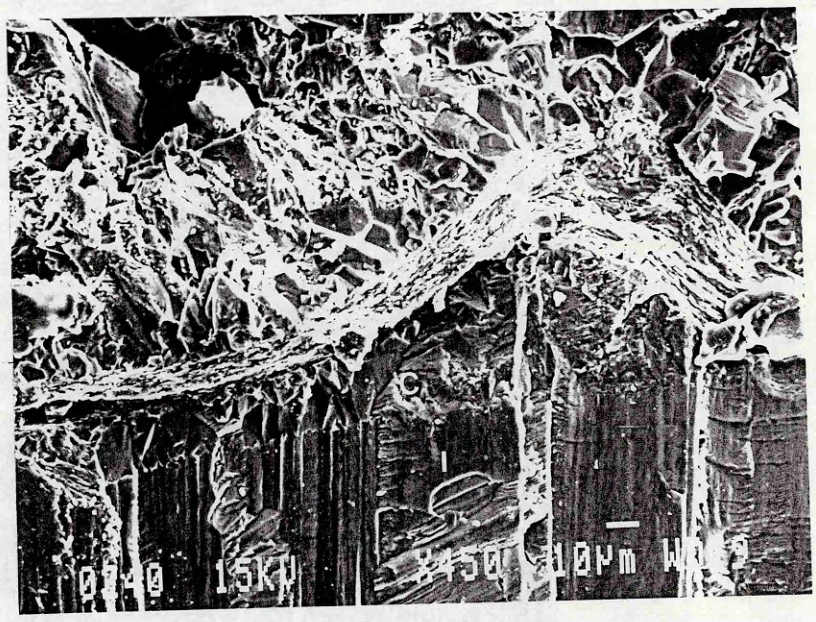


Figure 3.18: Fracture through *Atreta* (top) attached to *Inoceramus* (bottom), Stub EMH0240. Specimen collected from the Lower Gault at Munday's Hill, near Leighton Buzzard. I=*Inoceramus*, C=cement, F=foliated calcite of the *Atreta* and R=recrystallised aragonite?

3.3.2.3 Elemental analysis of the cement of *Crassostrea gigas*

The cement illustrated and described in the preceding section has a crystalline appearance. Evidence offered in Section 3.2.4 has already suggested that this cement is not a mucopolysaccharide but mineralised. It would seem reasonable to propose that it is calcareous. Confirmation of this has been sought by direct microanalysis. The small volumes of cement present make classic analytical techniques such as staining and XRD impractical. No technique is currently available to extract the cement without contamination from either substrate or shell. It was therefore necessary to analyse the material in situ using SEM and Energy Dispersive X-ray microanalysis (KEVEX). The technique, described by Goldstein et al. (1981), utilises the SEM to bombard an unknown material with electrons. The energy and relative abundances of X-rays emitted may be used to characterise the elemental composition of the subject. Since it is possible to sample areas $<1\mu m^2$, the technique can be used to analyse the composition of the cement without contamination by stray X-rays from either substrate or shell.

Materials

Since particles from the substratum may be incorporated in to the cement (see Figure 3.16), it was necessary to utilise a substrate whose entrapment would not lead to erroneous conclusions. In particular it was crucial that the substrate contained no calcium, which if incorporated into the cement, might suggest a higher level of cement calcification than is correct. This requirement excludes most substrates which are easy to fracture, including glass and most plastics. Polyetheretherylketone (PEEK) presents a suitable option. Roughened PEEK was used as spatting plates for *Crassostrea gigas*, obtained from Seasalter Shellfisheries. As before, at six weeks after settlement preparations were made of fracture across the left valve and the substrate. Mounted on carbon discs, but uncoated, these were examined under SEM

and areas of the prismatic calcite of the shell, the cement and the PEEK were analysed using the KEVEX elemental analysis software.

Results (Figure 3.19)

(i) PEEK

The spectrum obtained for the PEEK substrate is illustrated in figure 3.19(b). The largest peaks present represent those of sulphur and oxygen, with very little calcium, sodium, magnesium, silicon and aluminium. This emphasises the point that any contamination of the cement by engulfment of the substrate, will not significantly affect the amount of calcium recorded in the cement.

(ii) Oyster shell

It should be stressed from the outset that spectra taken from different points of the shell of the same individual oyster are often very different. This is not unduly surprising as it should be expected that the composition of the extrapallial fluid may vary during life.

Analysis of the prismatic calcite of the oyster shell reveals the high calcium and oxygen peaks expected of calcium carbonate (Figure 3.19(c)). Minor amounts of sodium, potassium, magnesium, phosphorus and chlorine may be attributed to association with seawater. Of interest is the high values of aluminium and zinc recorded. Perusal of the average elemental composition of seawater given by Kaye and Laby (1968) shows the amount of aluminium present is very small, 0.16 - 0.19 ppm. Since the extrapallial fluid, from which the shell crystallises, is ultimately derived from seawater (see Section 1.3.2), one would expect the aluminium values in the shell to be in agreement to that of seawater. Indeed, Galtsoff (1964) cites only trace levels in the shells of *Crassostrea virginica*; however, he does note that other authors have recorded levels as high as 200ppm in old shells contaminated by argillites trapped in the chambers. Is a high concentration of aluminium characteristic of the species *Crassostrea gigas*? Conspecifics supplied by the MAFF in Conwy were analysed in the same way,

producing only a negligible aluminium peak. Thus the high levels of the Al^{3+} recorded in the Seasalter oysters may be regarded as atypical, perhaps due to high aluminium concentrations present in the seawater due to filtration methods or derived from the settlement tank itself. Although unexpected, the high aluminium content provides a useful signature for a recognition of the oyster calcite.

(iii) Cement

The spectrum of the cement (Figure 3.19(d)) has principal peaks of calcium, oxygen, zinc and aluminium, with minor peaks of sodium, phosphorus, magnesium and chlorine. In virtually all respects the spectrum is identical to that obtained for the oyster calcite.

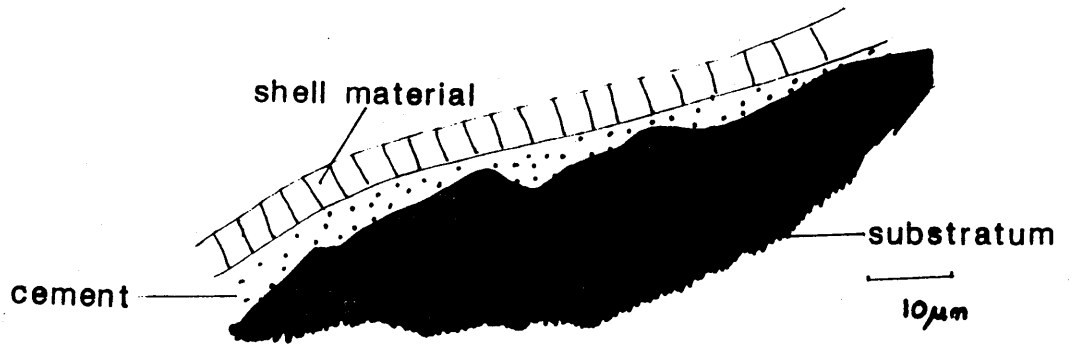
Discussion

Elemental analysis confirms that the cement is calcareous. The similar spectra of both cement and oyster shell strongly suggests that they share a common origin. Unfortunately, at this time there is no technique available to determine whether this cement is calcite or aragonite. My tentative assumption is that the cement is calcitic. This assumption is based on the similarity of the spectra for the oyster calcite and the cement, and the fact that the latter appears to derive from the same extrapallial fluid as the former. However the volume of cement present is insufficient to allow accurate extraction and determination of mineralogy by conventional XRD. Staining with Feigl's solution is even less practical. At the present it would seem that there are no satisfactory means of determining the mineralogy of the cement with the material and techniques which are available. It should be possible to distinguish between calcium carbonate polymorphs on the basis of crystal symmetry, calcite being trigonal and aragonite orthorhombic. However, such determination depends on the finding and identification of euhedral crystals. According to Bathurst (1975) the aragonite has higher strontium levels and lower magnesium levels than calcite because of the their varying tolerances to alien ions in their crystal lattices. It is clear, therefore, that

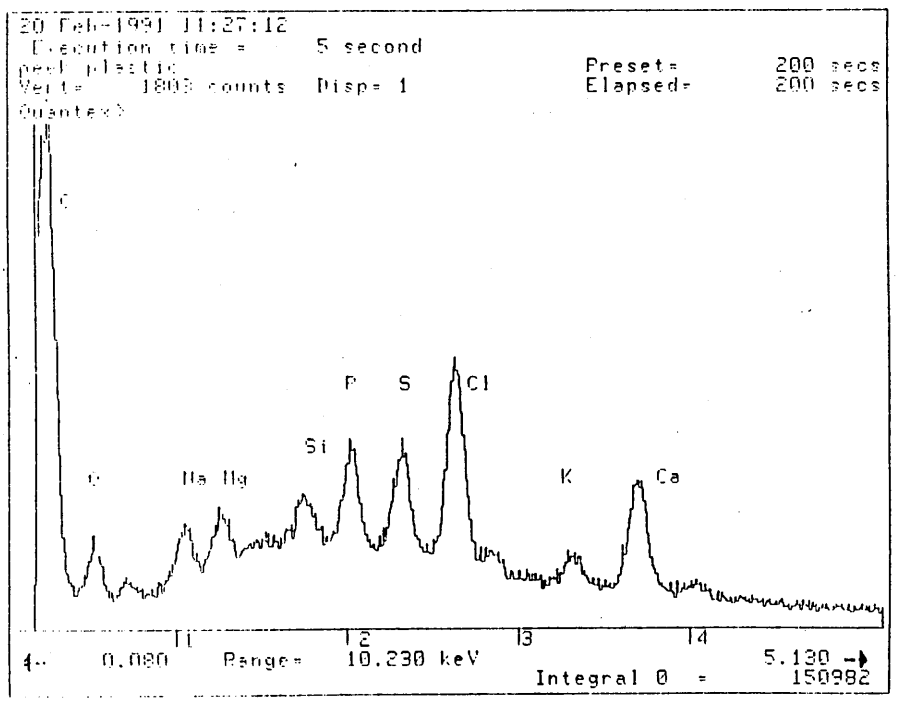
elemental analysis can be used to identify the two polymorphs. Yet here again its precise use is prohibited by the small volumes of cement present. The extreme similarity of the spectra achieved suggests that the composition of the cement and shell material, even with respect to minor elements, is identical. Although it is possible to sample the bulk composition of the cement in this way, the spread of X-rays and presence of contaminant particles within the cement would make determinations from very small areas, i.e. a single crystal, unreliable.

Figure 3.19: Elemental micro-analysis of the *Crassostrea gigas* cement. (a) Location map of analysis sites, (b) Spectrum for the substratum, (c) Spectrum for the outer prismatic layer of the oyster and (d) Spectrum for the cavity fill cement.

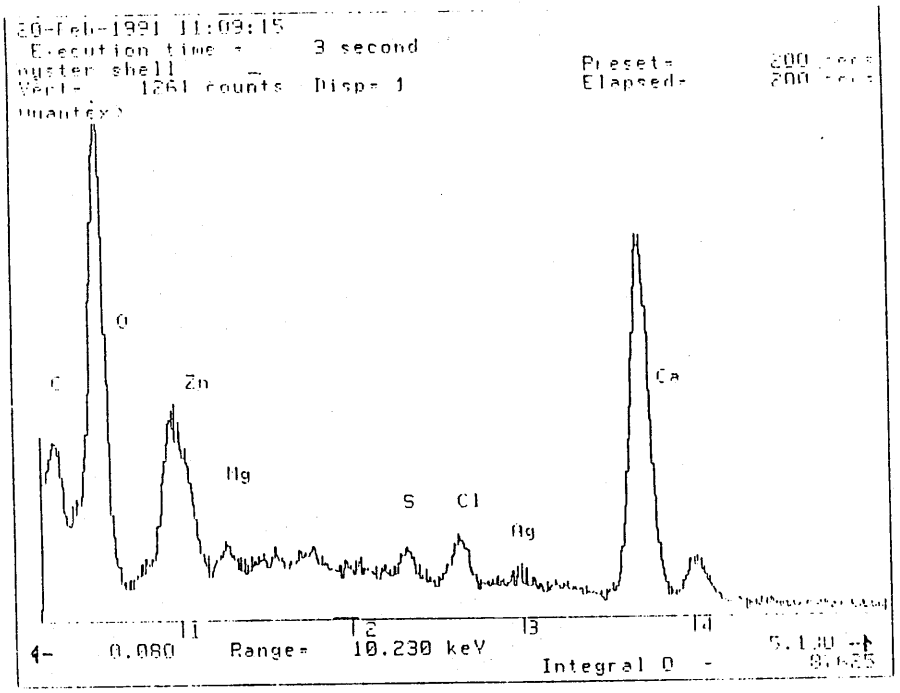
a)



b)



c)


20-Feb-1991 11:09:15
3 second
Preset=
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C
O
Zn
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10.230 keV
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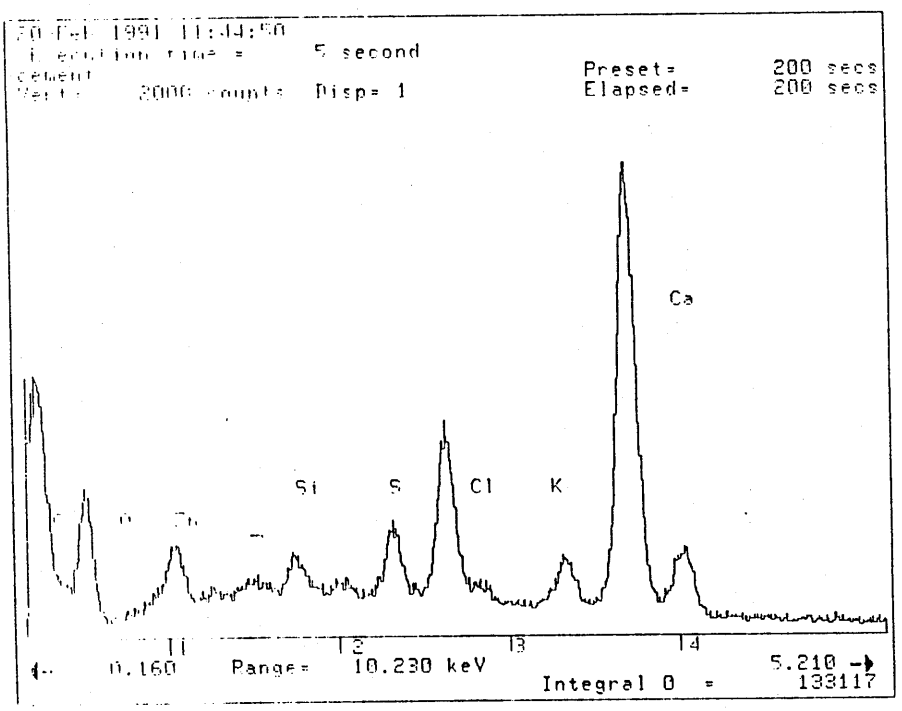
d)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Ca
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Range=
10.230 keV
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133117

3.4 INTERPRETATION OF RESULTS AND OBSERVATIONS

3.4.1 Proposed mechanism of cementation

Having made an extensive study of the key features involved in cementation in bivalves, it is now possible to comment on the validity of the hypothetical models suggested in Section 3.2.2 and to propose a mechanism for bivalve cementation. This section ignores cementation in the Chamacea, which is dealt with separately in Section 3.5.

As illustrated in Section 3.2.3 periostracum is continuously secreted during attachment in each of the living cementers studied. Therefore Model 1, that of direct shell secretion, may be rejected.

The possession of a thin periostracum, secreted as a solid sheet of uniform thickness is a universal feature of all. This negates Model 2, which postulates attachment by a fluid periostracum. The fact that microscopic examination of the contact between the substrate and shell has shown no significant spacing between the two suggests that the interdigitation model, proposed as Model 5, is unlikely to be the main mechanism of cementation. Interdigitation might be considered a valid mechanism for the specimen of *Myochama* described in Section 3.3.2.2. The interdigitating processes are not composed of shell material, however, and are clearly an external cement feature and hence cannot really be regarded as supporting the model. Nevertheless, the possibility that interlocking of the idiomorphic ornament of the bivalve and the substratum may have a role in certain circumstances is discussed in Chapter 5, in relation to the Pectinidae.

The observations from the preceding investigation appear to support Models 3 and 4. In most cases it has been possible to identify a crystalline cement between valve and substrate, clearly implicating the fourth model. Studies of the composition of the cement of the oyster, *Crassostrea gigas*, have revealed a remarkable similarity between it and the actual material of the shell. This observation, along with that of the textures observed within the cement, are critical to the development of the following argument.

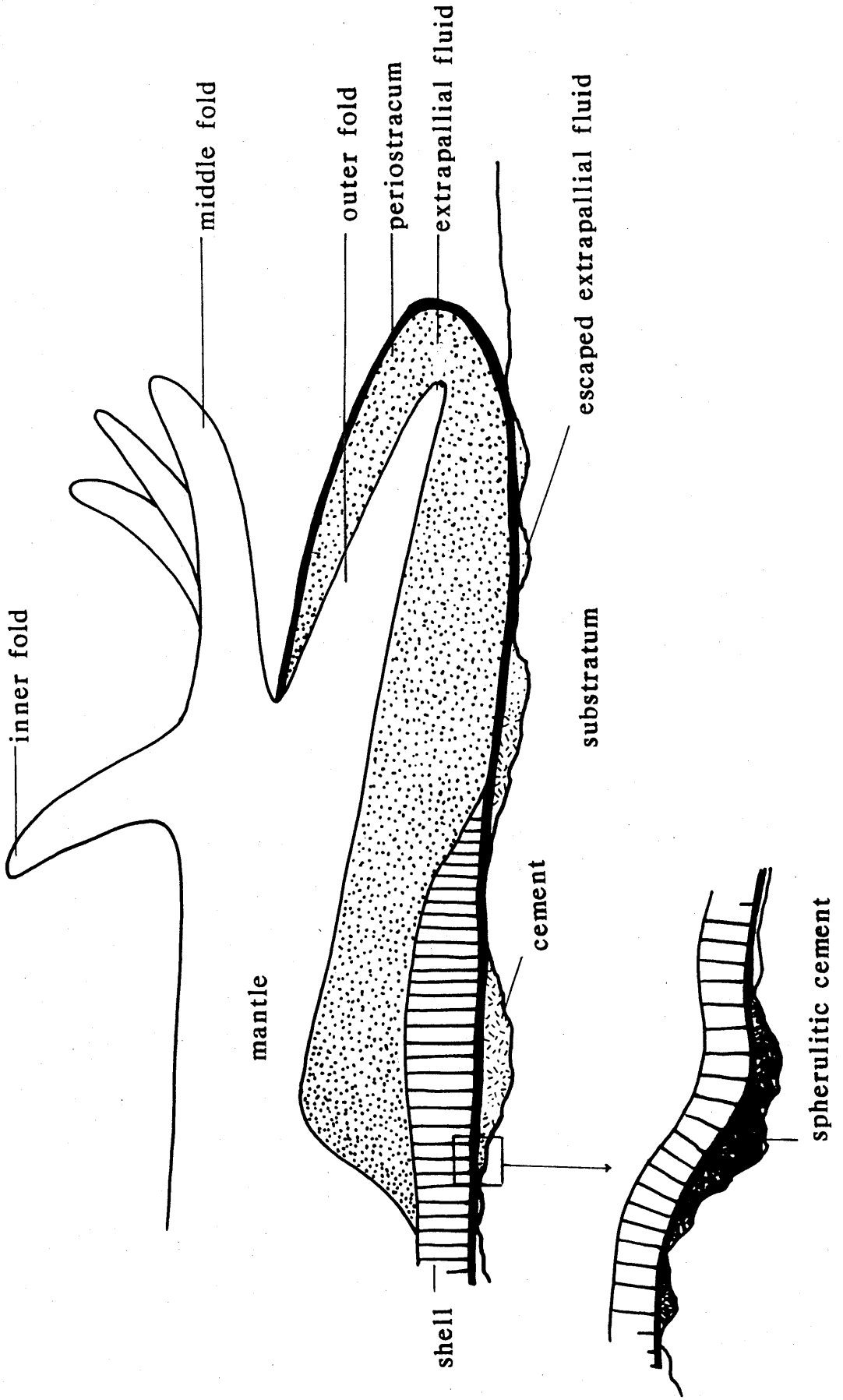


Figure 3.20: Simplified section through the ventral valve margins of a generalised cementing bivalve to illustrate the proposed mechanism for cementation.

Figure 3.20 depicts the ventral valve margins of a generalised cementing bivalve, as an attempt to illustrate the proposed mechanism of cementation. In order to produce a shell which closely mimics surface topography, the mantle margins require to be highly extensible so that they may add shell material not just to the valve margins, but also to the substratum as well. The genetic control of idiomorphic valve growth must be suspended, as illustrated in Figure 3.1, in order for the mantle to be effectively draped over the attachment surface. Once the mantle margins are brought into close proximity with the substratum, the thin flexible periostracum may be rolled out directly onto the surface. This *solid* sheet will not adhere directly, due to insufficient closeness of contact. Instead cementation is effected by crystallisation of extrapallial fluid which has escaped the extrapallial cavity, via a permeable periostracum, to lie between the valve and the substratum. The accumulation of this fluid performs the role of a smoothing agent to allow the two bodies to adhere. Freed from the biotic constraints on crystallisation, enforced by the periostracum and the mantle cells, the Ca^{2+} rich fluid is able to crystallise calcium carbonate in the form of a cavity fill cement, analogous to those observed on a larger scale in diagenetic cements, with spherulites nucleating on all available surfaces.

This mechanism is most easily reconciled with the pandoracean cementers, *Myochama* and *Cleidothaerus*, which plainly possess periostracal micropores, and also with the Etheriidae, if we accept Gregoire's (1974) observation of a loose mesh work structure in the periostracum of *Etheria elliptica* . These features would surely permit the passage of extrapallial fluid from the extrapallial cavity to the external environment. The remaining groups apparently have a solid periostracum, with no demonstrable channels along which the fluid could escape. Nevertheless, it has been independently shown that certain bivalves, including the oyster *Crassostrea virginica*, do possess mechanisms for the transfer of fluid from the extrapallial cavity to the external medium (Wilbur, 1964). Since the periostracum is a tanned organic structure, the transfer of material across its barrier must be by passive rather than active transport. There are at

least two possible mechanisms which might explain the leakage; firstly the periostracum may be porous at a resolution higher than is available in this study, or alternatively the sheet may be permeable or semipermeable at the molecular level, the large structural proteins which make up the periostracum being sieve-like. In any case in order to achieve transport of calcium and carbonate ions the minimum size of hole required is miniscule; the ionic radii are both less than 0.1nm, and even allowing for increased size due to co-ordination of water molecules, although obviously for the production of significant volumes of cement this size must be exceeded.

Future work is envisaged to investigate this problem of periostracum permeability. The use of TEM may enhance understanding of the structure of periostraca, but this will necessitate finding an improved method of isolating it, without physical damage. It is hoped that it will be possible to sample the cementing fluid below the periostracum, in order to make comparative analyses with the extrapallial fluid. In this way it will be possible to determine how selective this transport may be.

3.4.2 How widespread is this form of biomineralisation?

Although a novel discovery in the Mollusca, this 'inorganic' type of growth of biogenic minerals has been reported in other taxa. Constanz (1986) describes the growth of scleractinian corals by crystallisation of spherulites from a supersaturated fluid underneath the calicoblastic epithelium. Although Constanz believes that this process may be biologically mediated by the coral-algae symbiosis, he considers the growth of spherulites, resembling abiotic diagenetic cements, to be governed by physiochemical processes. Constanz suggests that comparable growth occurs in barnacles and coccoliths. Wood (in press) also reports similar growth textures in demosponges.

The controls and mechanisms by which organisms biomineralize is now recognised to be fundamentally important to evolutionary processes, in particular the evolution of hardparts. In terms of biomineralisation processes previously described, the

mechanism described here is relatively simple. The only requirement is for a marine organism to isolate a volume of a supersaturated fluid from the poisoning effects of seawater (see p.269). There is no necessity for the provision of an organic framework onto which the crystallites nucleate. The convergent evolution of this form of biomineralization in many taxa underlines the ease with which it may be attained. The discovery, in this thesis, of its involvement in the cemented habit has obvious implications not only for the evolution of cementation in other taxa (see Section 7.5) but also for biomineralization as a whole.

3.5 CEMENTATION IN THE CHAMACEA

Members of the Chamacea were excluded from the above discussion because of the apparent ease of separation induced by organic dissolution. This weaker mode of attachment seems to imply that the model of attachment by crystallisation of extrapallial fluid beyond the periostracum is invalid in this case. Which of the hypothetical models is supported?

The presence of a fine periostracum illustrated in Figure 3.5(K) eliminates Model 1, whereas the fine, solid, uniform thickness (<1μm) displayed by this specimen is evidence of the nonapplicability of Model 2. Extensive SEM searches of the contact between the cemented valve of *Chama* and its substratum have failed to reveal any sign of an external cement. The periostracum appears to lie perfectly along the surface of the substratum, thus implicating Model 3, suggesting that *Chama* is able to adhere simply by producing a shell in very close contact to the substrate. However, caution must be expressed over this conclusion. As noted previously, there are a number of difficulties inherent in studying contact on natural substrates. Material used here is exclusively attached to coral, which severely complicates the attachment surface. In order to verify the conclusions reached here, future work is envisaged obtaining *Chama* spat on glass substrates.

The fact remains, however, that the attachment of *Chama* is weak and organic-based. Investigation of the fossil material in the NHP and Bristol City Musem (acc. no. 103/1946) has revealed that few fossilise still attached to their substrates. Of 302 specimens, ranging in age from Palaeocene to Quaternary, examined for signs of attached substrata, only 40, a mere 13%, displayed substrate remains (e.g. NHP L 8507 Miocene *Chama gryphoides* attached to a coral), the remainder have no vestige of a substrate. However the non-attached individuals clearly *were* attached in life, as the recognisable attachment scars of corals, gastropods and conspecifics attest (see Figure 3.21).

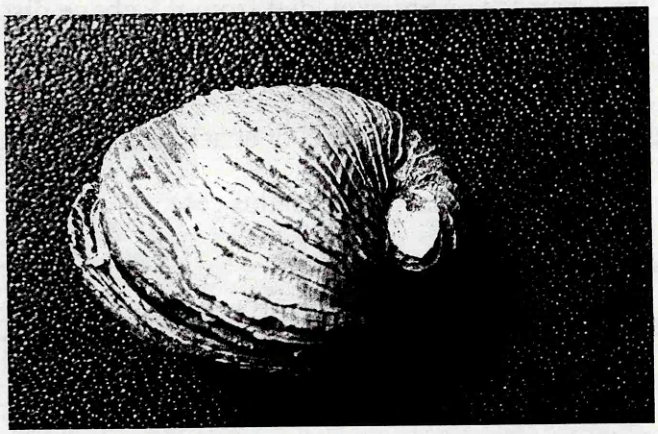


Figure 3.21: *Chama squamosa* with clear attachment scar but no remains of the substratum. NHP specimen, unregistered, collected from the *Chama* Bed, Barton (Eocene). Valve height=32mm.

Analysis of the relative numbers of attached and non-attached specimens, for each stratigraphic interval is given in Table 3.3. The attached percentage is consistently low except for those of Pliocene and Palaeocene age. However, the relatively high percentages recorded for these (37.5% and 29% respectively), may be attributed to the small sample size, rather than real increase.

AGE	NO. ATTACHED	NO. DETACHED	% ATTACHED
QUATERNARY	0	4	0
PLEISTOCENE	2	17	12
PLIOCENE	6	16	37.5
MIOCENE	3	44	7
OLIGOCENE	8	49	16
EOCENE	14	85	16
PALAEOCENE	2	7	29
NO AGE DATA	5	40	12.5

TABLE 3.3 Survey of the relative numbers of attached and detached fossil *Chama*. N=302.

There are four possible explanations to account for the low percentage of attached specimens in the fossil record:

(i) *Collection bias*

It might be argued that cemented bivalves attached to substrata are cumbersome and will thus be discriminated against by the collector in favour of more compact unattached specimens. Although this may be true in some instances, it is unlikely in this case. Most *Chama* observed either are, or were, attached to relatively small substrates, such as gastropods and conspecifics, which cannot be described as unwieldy. Additionally the specimens investigated were collected by a plethora of palaeontologists from a multitude of localities, tending to nullify the biases of individual collectors.

(ii) *Classification problems*

A potential problem exists with looking at museum collections is that attached cementing bivalves may be regarded as fouling epifauna, with the result that specimens will be catalogued according to substrate taxa. However, searches for *Chama* in other collections of Barton Clay and Crag specimens yielded nothing, although the

possibility remains that attached specimens may have been removed by overzealous preparation.

(iii) *Dissolution of substrates*

Attached substrates may have been lost by dissolution during diagenesis. However, the abundance of both polymorphs of calcium carbonate in the deposits in which the *Chama*, have been collected suggests this as unlikely.

(iv) *Weak original attachment*

A weak attachment of periostracal origin, may be easily sundered on death by taphonomic processes of bacterial decay. This point is demonstrated in Section 3.2.4. This is considered to be the most plausible explanation of the low percentage of attached *Chama* in the fossil record.

3.6 WHAT DOES THIS STUDY ON LIVING CEMENTING BIVALVES IMPLY ABOUT THE EVOLUTION OF THE HABIT?

Identifying requirements for cementation

Now that I have established the means by which modern bivalves cement it is possible to identify the conditions which need to be fulfilled in order for a bivalve to cement. These are as follows;

- the ability to construct a shell which follows substrate topography.
- the production of a permeable periostracum.
- the ability to lay that periostracum down in close proximity to the attachment surface.

The following chapter deals in detail with the way in which members of the clades which gave rise to the various cementing bivalves were preadapted, both structurally and behaviourally, so allowing them to have achieved the above.

3.7 CONCLUSIONS

1] Cementation must involve some modification to the basic shell secreting processes.

2] Five hypothetical models may be put forward to account for the mechanism of cementation in bivalves. These models may be distinguished simply by study of the nature of the periostracum and the detail of the contact zone.

3] In all living bivalves a periostracum is secreted continuously during the cementation process. This is also likely have been the case for extinct clades. This periostracum is solid and maintains a constant thickness. Compared to most non-cementing bivalves the periostracum of cementers is ultrathin, in most cases less than 1μm. The presence of periostracal pores has been demonstrated in *Myochama* and *Cleidothaerus*.

4] In all but the Chamacea the cemented bond is not broken by removal of organic matter, implying that the cement is mineralised.

5] Detailed examination of the cement of the dissoconch of *Crassostrea gigas* reveals that a calcareous cement grows between valve and substrate in a form resembling abiotic diagenetic cements. Similar textures are recorded in other bivalve taxa.

6] The interpretation of the above results is that cementation in the vast majority of living bivalves occurs by leakage of extrapallial fluid to crystallise beyond the normal confines of the periostracum. Such crystallisation is under the control of physiochemical factors rather than an organic matrix. This mode of biomineralisation has been demonstrated, by other authors, to be utilised in totally separate taxa, e.g. scleractinians and demosponges. This evolution of this simple means of precipitation of biogenic minerals is clearly convergent.

7] It is assumed that the cement has the same mineralogy as the outer shell layers, and presumably varies from one clade to another.

8] The cemented bond of the Chamacea is easily sundered by removal of organic material. Investigation of palaeontological material suggests that the means of this attachment in this superfamily has always been weak , easily broken by taphonomic processes. The proportion of fossil *Chama* preserved attached to substrata is low.

CHAPTER 4

PREADAPTATIONS TO CEMENTATION: EXTRAPOLATION IN THE FOSSIL RECORD

4.1 INTRODUCTION

The origins of many cemented bivalve clades are obscure. In order to make sensible suggestions as to which groups could potentially have been ancestral to cemented stocks, it is necessary to utilise the information provided by the previous chapter. Chapter 3 established the mechanism of cementation in modern bivalves. In the vast majority it is crystallisation of a cement from extrapallial fluid *outside* the periostracum, between the valve and substratum, which is of critical importance. Accordingly it should now be possible to suggest what attributes are required for this mode of cementation to evolve. The aim of this chapter is to explore these preadaptations and other adaptations to cementation with a view to being able to recognise and catalogue them in the fossil record.

4.1.1 Preadaptation

Skelton (1989) defines preadaptation as "..... a feature or a complex of features of an organism, whether already serving a functional role or merely a constructional product, which by virtue of its *fortuitous* suitability for novel functional effects, becomes *co-opted* as a new adaptation ... in descendents of the organism." (my italics).

Gould and Lewontin (1979) have challenged the adaptationist programme as unscientific, generating untestable hypotheses. However, Skelton (1985) defends the concept of preadaptation, imploring that preadaptive hypotheses should be tested by retrodictions. He demonstrates this with a rigorous test of the hypothesis that shortening and invagination of the ligament led to the extensive radiation of uncoiled

rudists.

Section 3.5.1 outlines the general requirements for cementation, namely a thin periostracum, at least semi-permeable, and the ability to lay that periostracum across a hard substratum. One might predict that those bivalves which possess thin periostraca and construct their valves close to hard surfaces are preadapted for cementation. Only minor changes to the character of the periostracum and shell secreting mechanism are needed to allow cementation. How do we recognise such preadaptations in the fossil record?

4.1.2 Adaptations to the habit

Assuming that cementation confers selective advantage (see Chapter 6), one would intuitively predict that natural selection would favour the evolution of adaptations which facilitate the habit. One of the problems in studying these is to distinguish them from preadaptations. It is quite conceivable that a novel adaptive feature in one clade may have been preadaptive in another.

4.1.3 The fossil record

If we are to be able to identify preadaptive features and use them to trace the evolution of the habit in a clade, we have to be able to identify or infer these features in fossil material. Therefore, for each of the features discussed in this chapter an assessment is made of its 'traceability' in the fossil record. Where applicable, examples of pilot studies are also given.

There are a number of problems with looking at the fossil material:

(i) *Loss of soft parts*

It is clear that most of the adaptations for cementation will be concerned with the mantle margins, and hence normal taphonomic processes will limit available data.

(ii) *Diagenetic loss of aragonite*

Dissolution of aragonite during diagenesis frequently results in the loss of at least the inner shell layer, depriving us of such indirect information about soft parts as may be available, e.g. pallial myostraca.

(iii) *Stylolitization*

Pressure solution surfaces between the cementing bivalve and its substrate obliterate details of the cemented zones.

4.2 APPROACH

The general approach of this chapter has been to try to find ways in which the observations I have made from the living material can be translated to fossils, thus enabling a greater understanding of the evolution of cementation. The work outlined here is incomplete; it revolves around ideas which have potential use. It is not anticipated that all these ideas will be applicable to all clades. Nevertheless this chapter represents a first order attempt to find useful lines of enquiry to follow. Such a construction of windmills for others to tilt at is valid science. For example, Section 4.5.1 discusses the possibility of extracting information about the periostracum from the fossil record. The periostracum is a fundamental part not only of the bivalves but also of all other molluscs, so information as to its evolution will be critical to our understanding of the development of molluscan biomineralisation. Yet we are ignorant of the fossil record of this organic structure.

The work presented here is divided into three major sections:

(i) *'Behavioural'* preadaptations which bring the animal into the life position in which it might cement,

(ii) *Constructional* features which actually allow cementation to occur,

(iii) *Environmental* changes which facilitate the cementation process.

4.3 'BEHAVIOURAL' PREADAPTATIONS

A fundamental requirement for cementation is that the mantle margins must be brought in to close proximity with a hard substratum in order that shell/substrate overgrowth can occur.

4.3.1 Pleurothesis and the valve of attachment

Yonge (1979) argued that cementation requires "the prior assumption of a pleurothetic

habit". This is an obvious way to bring the mantle margins into contact with the substrate. Yonge's thesis can, however, be taken much further to give useful information about putative ancestory.

LEFT	LEFT or RIGHT	RIGHT
OSTREACEA	CHAMACEA	PECTINIDAE (4 clades)
	ETHERIIDAE (3 clades?)	SPONDYLIDAE
	HIPPURITACEA†	TERQUEMIIDAE
		DIMYACEA
		PLICATULACEA
		CLEIDOTHAERIDAE
		MYOCHAMIDAE
		LITHIOTIDAE
		ANOMIIDAE
		PSEUDOMONOTIDAE
		CHONDRODONTIDAE

Table 4.1: Identification of the valve by which members of each clade cement. Data from Section 2.3.3. † although rudists may attach by either left or right valve they do so consistently within a genus.

Table 4.1 identifies by which valve each of the various clades attaches. On the basis of this the cementing bivalves may be divided immediately into the two groups below:

(i) *Constant valve of attachment*

The vast majority of cementers attach constantly by one valve. Only the Ostreacea adhere by the left valve, the remainder cement by the right. There are two possible reasons for this consistency in each clade:

-The clade is derived from pleurothetic stock.

-Only one of the mantle lobes possesses the modifications to shell formation necessary to enable cementation.

For those clades of known origins it is the former explanation which is favoured, although it is accepted that in these cases the 'upper' mantle lobe may also lack the ability to cement. For example, all Pectinacea are dextrally pleurothetic, so it is unsurprising that all representatives which cement (Spondylidae and four clades within the Pectinidae) do so by the right valve. It has long been demonstrated that the members of this superfamily possess statocysts which enable the organism to detect and maintain this orientation. It would appear, therefore, that constancy of one valve of attachment is heritable and gives some indication of a previously pleurothetic ancestry. If the second explanation were true it might follow that in an early evolutionary stage we might see a species exhibiting two morphs; one cementing by one of the valves and a second free lying on the other. Subsequent evolution might allow these morphs to diverge. Although this scenario appears inapplicable to most of the cementing clades it has potential interest in the evolution of the Myochamidae. Section 2.3.3.13 described the dichotomy within this family between cementers and non-cementers and the symmetries of their valves.

(ii) *Left or right valve of attachment*

Three clades have the ability to cement by either valve; the Etheriidae, Chamacea and Hippuritacea. However, this group can be further subdivided into two:

a) The etheriids and chamids are truly indifferent in the valve by which they attach. Even within a single species individuals may cement by either left or right valves. The implication of this is that *both* mantle lobes have the modifications necessary to cement and that chance dictates the valve used for attachment. Any differences between attached and non-attached valves, therefore, arises through ontogeny rather than being genetically predetermined. La Barbera and Chanley (1971) describe the pediveliger of *Chama congregata* as orthothetic and equivalve before toppling over, at which point cementation and asymmetry ensues; they do not , however, acknowlege the possibility that this may be by either valve. Yonge (1978a) implies a similar scenario for *Etheria*, but the ontogeny of this genus has never been properly studied.

The fact that these living bivalves may cement by either valve implies not only that

both mantle lobes have the capability to effect cementation but also that they derive from orthothetic stocks. Indeed the suggested origins for both these clades, from within the Carditacaea for the chamids (Kennedy, Morris and Taylor, 1970) and the Unionidae for the Etheriidae (Yonge, 1978a), are orthothetic.

b) Although rudists may cement by the right or left valve each genus displayed consistent attachment by one or the other. The explanation of this is rather more problematic than for the chamids and etheriids. Skelton (1978) indicates that the ancestors of the rudists, the Megalodontacea, were primarily orthothetic. However, certain megalodonts, e.g. *Neomegalodon*, were more inequivalve and probably had a tendency to be ballasted towards one valve or the other (Skelton, personal communication). This may suggest that, although the megalodontids as a whole may have had both mantle lobes predisposed for cementation, this was only exploited in forms with a bias towards pleurothesis. This might imply that the cemented habit did arise twice within the Hippuritacea as separate innovations from left and right valve biased megalodonts. However, there is little direct evidence from the fossil record to support this. There is a critical gap between the Liassic and Oxfordian where there are no reports of megalodontids which might be plausible candidates for the most immediate ancestors of the rudists, (Skelton, personal communication). After this gap the cementing rudists appear for the first time, clearly differentiated into right valve cementing (*Diceras*) and left valve cementing (*Epidiceras*) genera. Clearly, there is a requirement for further collections to be made from rocks of the critical age, in order to resolve this debate.

4.3.2 Ontogenetic habit changes and stage of attachment

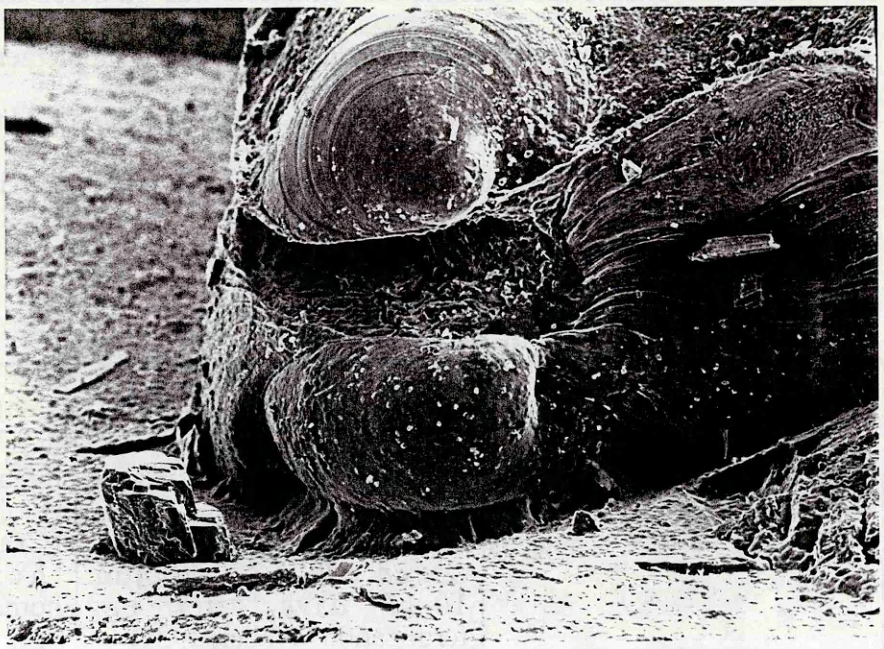
A study has been made of the pre-attachment stages of living cementing bivalves in an effort to establish the ontogenetic stage at which cementation occurs and to determine whether these phases are byssate. Information was gathered mostly from SEM examination of the juvenile portions of cementing valves, supplemented by additional information from the literature. For *Hinnites giganteus* and *Chlamys pusio* direct observations of individuals prior to cementation were possible. This information is given in Table 4.2.

CLADE	STAGE OF ATTACHMENT	BYSSATE PHASE?
Ostreacea	V. early. End of prodissoconch, see Figure 4.1(a). *Crassostrea gigas* 250µm. *Ostrea edulis*-250-300µm. 10-15 days after egg fertilization (Waller, 1981)	No evidence of byssal threads but the pedal cement is of identical composition (Cranfield, 1973a) and therefore maybe homologous.
Chlamys pusio	V. Late, after c. 2 years (see section 5.2.3) Av. valve height=16mm	Yes. Juvenile bears ctenoliate byssal notch.
Hinnites giganteus	V.Late in dissoconch, 1.5-2 years, See Figure 4.1(b).	As above.
Spondylidae	Early dissoconch. Height=1000µm, see Figure 4.1 (c).	Yes. Non ctenoliate byssal notch.
Dimyacea	End of prodissoconch/early dissoconch.	?
Plicatulacea	End of prodissoconch/early dissoconch	?
Cleidothaeridae	Dissoconch. Height=1200µm. See Figure 4.1(d).	No evidence of notch. Morton (1974) finds no byssal gland.
Myochamidae	Dissoconch. Height= 1300µm	No evidence of notch
Chamacea	Dissoconch. Height for *Chama congregata*=350µm (La Barbera &Chanley, 1971)	Yes. No notch, but La Barbera & Chanley note the presence of a fine byssal thread.
Etheriidae	Late dissoconch. *Acostaea lobata* height= 5000µm (Yonge, 1979).	?

Table 4.2: Stage of attachment and presence/absence of early byssate stages in living cementing bivalves.

Figure 4.1: Scanning electron micrograph of the pre-cementation phases of living cementing bivalves. (a) *Crassostrea gigas*, Stub EMH0293 (b) *Hinnites giganteus*, Stub EMH0252 (c) *Spondylus gaederopus* Stub EMH 0000and (d) *Cleidothaerus albidus* Stub EMH0316.

a)



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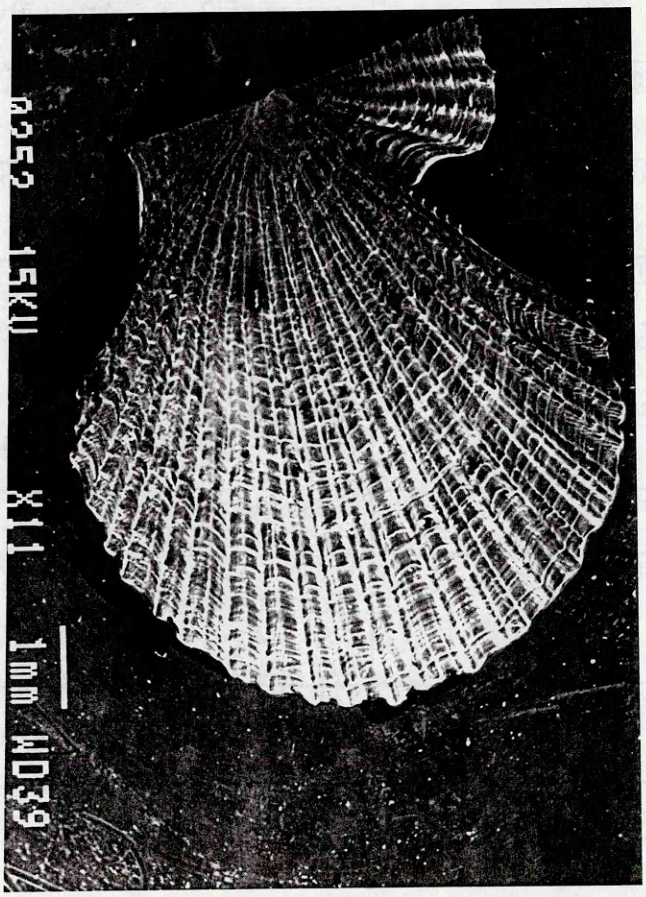

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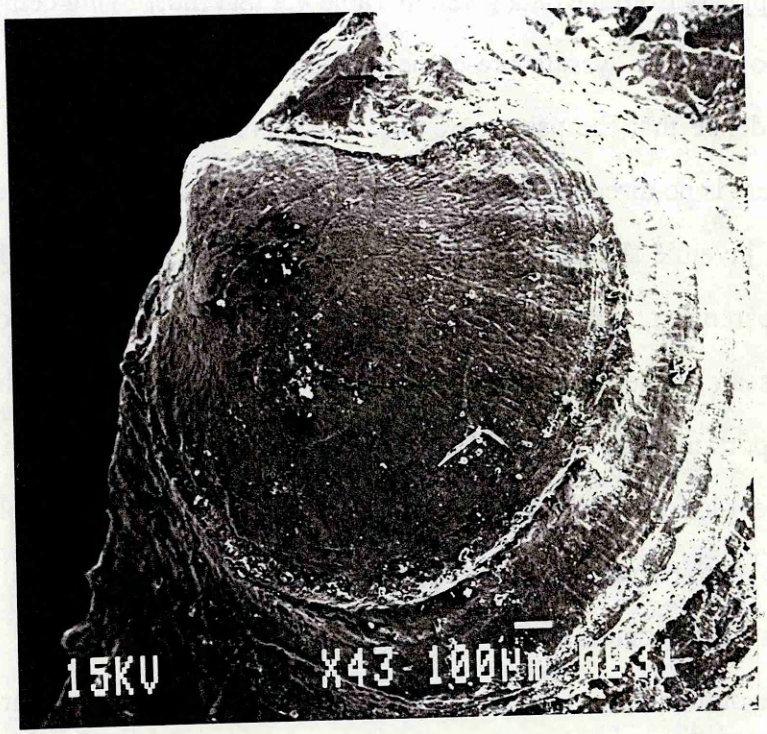

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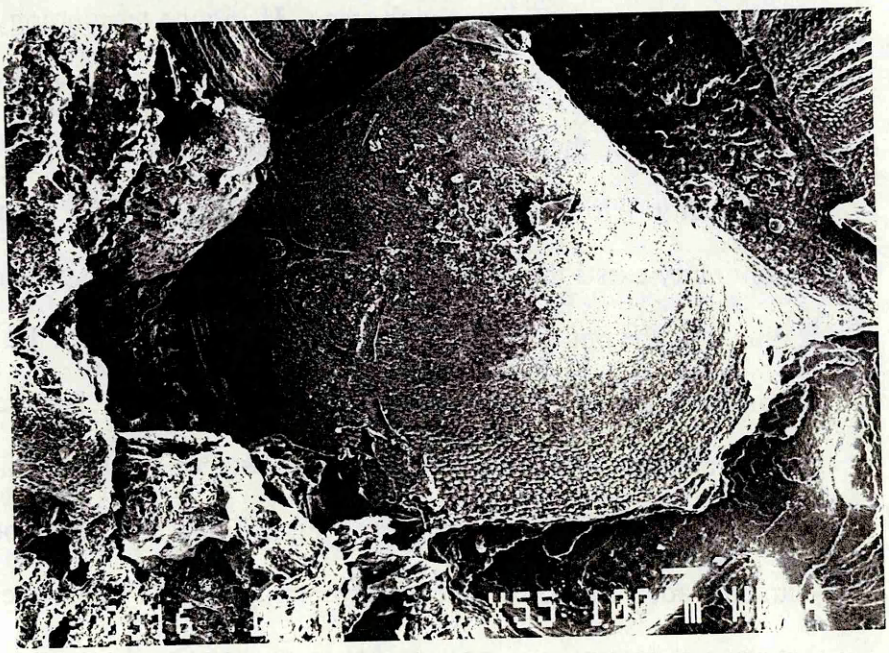


It appears from the data given in Table 4.2 that most living cementing bivalves have a recognisable byssate pre-cementation stage. Of the extinct clades there is good evidence that the pseudomonotids and terquemiids also had early byssate stages. There is no direct evidence of byssate attachment in rudists. Skelton (1976) illustrates the juvenile shell of a specimen, less than 1mm high, with a flattened anterior face apparently attached to the substrate. However, small megalodontids were probably byssate, (Skelton, 1978). I believe that the presence of this byssal stage is an important prerequisite to cementation both in terms of an individual's ontogeny and its evolution. Such attachment provides the bivalve with a stable orientation to enable the mantle margins to be applied to the substratum. The implication is that most, if not all, cementers evolved from byssate stocks.

The ontogenetic stage at which cementation occurs varies markedly between clades, from attachment at the close of the prodissoconch stage in oysters to its onset well into adult life (at 1.5-2 years) in *Hinnites* (Neil Bourne (Canadian Fisheries), personal communication). In the vast majority, attachment by cementation commences during the dissoconch stage. Using the terminology of Wrigley (1946), that adopted in the *Treatise*, dissoconch development can be divided into two stages. An early phase, the nepionic stage is defined as ending with a sharp growth discontinuity. However such a definition is useless here, for what greater growth discontinuity exists than the onset of cementation? At the present, the nomenclature dealing with the ontogeny of bivalves is not adequate to split the dissoconch phase so as to differentiate between 'early' and 'late' dissoconch attachment. On these grounds all these cementing bivalves can be categorised as attaching at the close of the nepionic stage, whether that be a matter of hours after the prodissoconch or many years into adult life. Until a better terminology can be established it is recommended that stage of cementation is referred to by quantifying the valve size of the termination of the nepionic stage.

To a certain extent the timing of cementation is subject to ecophenotypic variation (see data in Section 5.2.3 for *Chlamys pusio*). Permanent attachment may only proceed

when a hard substratum has been encountered. Although it is well known that the veliger larvae of oysters may rejoin the plankton if the substrate on which they have landed is inappropriate for permanent attachment (Cranfield, 1973(b)), the onset of cementation cannot be retarded indefinitely. Ukeles and Rose (1975) present evidence that veliger larvae of *Crassostrea virginica* maintained in high density cultures will adhere to one another in the plankton, and that this aberrant behaviour may be induced by the addition of antibiotics which accelerate the developmental programme. In addition Nelson (1924) reported initial cementation in *Crassostrea virginica* by the mantle, rather than by a pedal cement as discovered by Cranfield (1973(a)). Cranfield believes that the behaviour observed by Nelson may have been that of larvae which had been deprived of suitable substrates and whose development had run past the pedal stage of cementation.

Figure 4.2 plots the minimum length of geological time since cementation evolved in each clade against the stage in the life cycle at which living members cement (the stage in the life cycle at which cementation occurs has been assigned an ordinal value, higher numbers indicating later cementation). It must be stressed that the y-axis has been given arbitrary units and that the relative spacings between ontogenetic stage are not of equal duration.

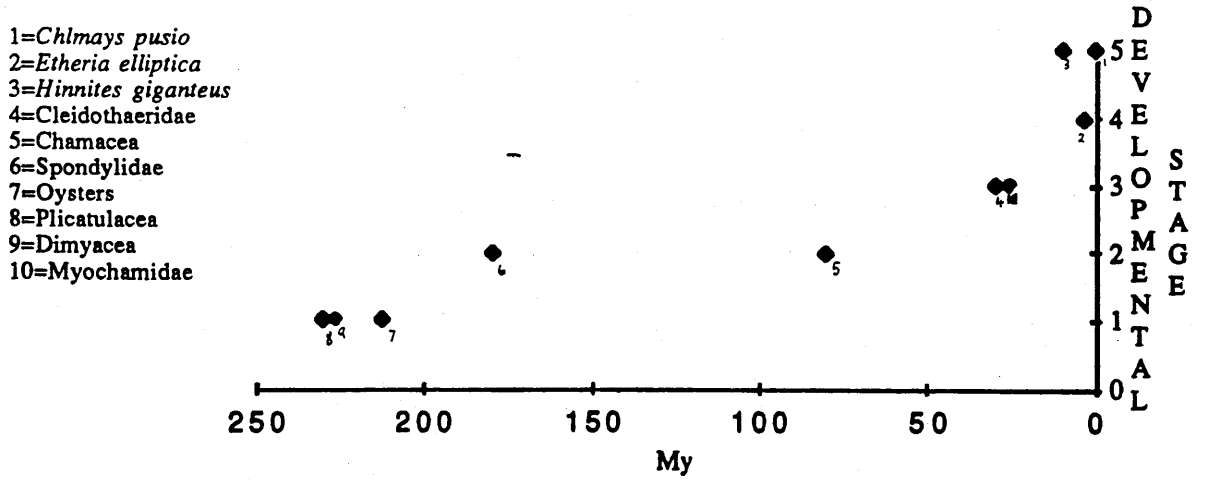


Figure 4.2: Ontogenetic stage of the onset of cementation in living bivalves plotted against their evolutionary longevity. 1=end of prodissoconch, 5= very late, > 1 year after settlement. Divisions 2-4 refer to division of the dissoconch on grounds of shell height at attachment; 2<1000μm, 3<2000μm and 4<10000μm.

The implication of the scatter graph is that members of those clades with longer evolutionary histories cement at earlier ontogenetic stages than do those from clades with shorter histories. Yonge (1979) also noted this apparent trend, but did not develop the theme. The suggestion is that selection pressures favour a gradual contraction of the 'free' pre-cementation phase. It is not intended that this graph should be construed as a trend with a definite gradient along which all cementing bivalves will pass over evolutionary time. It does not, for example, follow automatically that earliest oysters cemented at such late stages as are now observed in *Chlamys pusio*. It is merely the direction of this trend and its general implications which are perceived as important. The trend is repeated if the graph is plotted using valve height at attachment, rather than developmental stage, against evolutionary longevity. Although this may not take account of differing growth rates McNamara (1986) stresses that "size is often a convenient proxy" for the more difficult-to-establish growth stage. Before great evolutionary hypotheses are born of this observation it is necessary that the palaeontological data be collected.

A systematic examination of the timing of cementation in oysters, and of the factors which affect it, would be an entire research project of its own. There are several complicating features which inhibit collection of such data. These include diagenetic loss of the aragonitic juvenile stages, obscuring of the early growth stages by the later shell and the substrate, and the sheer number of examples required to nullify the effects of ecophenotypic variation. Nevertheless I have been able to collect evidence which supports the general premise that fossil oysters cemented at a later ontogenetic stage than their modern counterparts. This information is catalogued below, though possible alternative explanations for the observations are also suggested.

(i)- Surlyk and Christensen (1974) make the general comment that the Campanian Ivö Klack fauna contained abundant material of the oyster *Ostrea haliotoidea* of valve height over 5mm. My subsequent detailed inspection of substrates from Ivö Klack, held in Copenhagen, showed that not only were juveniles of this genus missing, but that there was a

marked absence of young individuals of the other oyster genera prevalent at the site. This lack of small attached oysters may indicate that these were not truly cemented or that recent spatfall had failed.

(ii)-Unpublished work by P. Palmer (personal communication) has established the presence of planktonic oyster larvae from the Kimmeridge Clay at a more advanced growth stage than in recent samples. Although this may support the hypothesis it must be noted that, during the deposition of these fine sediments, there may have been a general paucity of hard substrata available for colonisation. This may have led to delayed settlement.

If this speeding up of the developmental rate which governs attachment processes in cementing bivalves is genuine then this is an example of heterochrony. More specifically, using the terminology of McNamara (1986), this is an example of peramorphosis; the appearance of the ancestor's adult morphology in more juvenile descendents. McNamara describes three ways in which peramorphosis may be achieved; of these acceleration, the increase in rate of morphological development, would seem to be most appropriate.

This suggestion partially vindicates Jackson (1890), who implied the operation of heterochrony when he suggested his evolutionary lineage *Pecten-Hinnites-Spondylus-Plicatula.*

There is a clear need for future work in this area. The most promising avenue for further investigations is to examine spat bioimmured on the attachment surfaces of other oysters. Given that oysters are gregarious and that spat have a tendency to settle close to adults (Bayne, 1969) it is highly likely that many young oysters suffer the stifling fate of overgrowth, and thus preservation, by their elders. The increased interest in bioimmured organisms and expertise in splitting fossil oysters from their substrata are likely to provide ample data of spat development.

4.4 CONSTRUCTIONAL REQUIREMENTS AND ADAPTATIONS

The previous section has outlined the behavioural and developmental preadaptations which bring the mantle margins into close proximity to the substrate. Such orientation, however, does not guarantee cementation. There are large numbers of pleurothetic bivalves which have 'lower' valves closely adpressed to, and mimicking, the substrate topography but which do not cement. Section 3.5. identifies the critical changes which must occur to the construction of the bivalve in order to allow cementation. The most notable of these is the production of a thin, at least semi-permeable periostracum and the ability to place that periostracum close to, or directly onto, the substratum. These changes obviously largely involve soft parts. The outlook for being able to detect information about their evolution from the fossil record is gloomy. Even so, the aim of this section is to try to find ways in which these soft part modifications may be reflected in the hardpart morphology, as a starting point from which it may be possible to make progress in this relatively unpromising field.

4.4.1 The periostracum

The preservation potential of periostracum is very low. Even in the living mollusc, most species rapidly lose this organic layer through various agencies of physical or biotic abrasion, fungal attack and bacterial decay. Only those molluscs with thicker periostraca, such as the gastropod *Buccinum* and the bivalve Arcacea and Mytilacea show any great persistence of this sheet during life. Searches in palaeontological material at NHP have shown that even within these taxa preservation of periostracum is rare, examples being confined to Quaternary specimens (e.g. LL27096, *Anadara* collected from the Pleistocene of Alabama). Hudson (1968) describes the Jurassic mytilid *Praemytilus strathairdensis,* which has a structureless external layer, now calcitised, 5-15μm thick, which he interprets as periostracum, but such examples are rare.

It may be that the periostracum of the cemented valve of cementing bivalves may be in some ways protected from destruction. Thin sections occasionally reveal a thin

micritised layer between the cemented valve and its substrate, but at the moment it is unclear whether this is the remains of the periostracum or an integral part of the substratum. Notwithstanding this, it is most unlikely that features such as periostracal permeability will be directly recognisable in palaeontological material. But what hope is there of periostracal thickness determination, an item in which other authors have also expressed an interest in the context of evolution, e.g. Clark (1976)?

Estimation of periostracal thickness from the fossil record?

A possible method for inferring periostracal thickness from fossil material is described below.

The method I have adopted to approach this problem hinges largely on the primary function of periostracum; that of providing a template onto which the calcareous portion of the shell is secreted. It follows that any micro-ornament displayed by bivalves results from the configuration of the periostracum. Figure 4.3 shows two hypothetical models by which micro-ornament might be produced. In the first, the periostracum maintains a constant thickness and the ribbed shell ornament is achieved by folding of the sheet. The periostracum of the second model is of variable thickness and the inner surface of the sheet is sculptured to provide the negative of the ornament. In the course of the research for Chapter 3 the periostraca of 72 living bivalves were prepared and examined by SEM. All appeared to be of constant thickness and none displayed the form predicted by Model 2. Indeed it is difficult to envisage how such a periostracum could be manufactured. Micro-ornament must thus be produced by folding of the periostracal sheet, as suggested by Model 1.

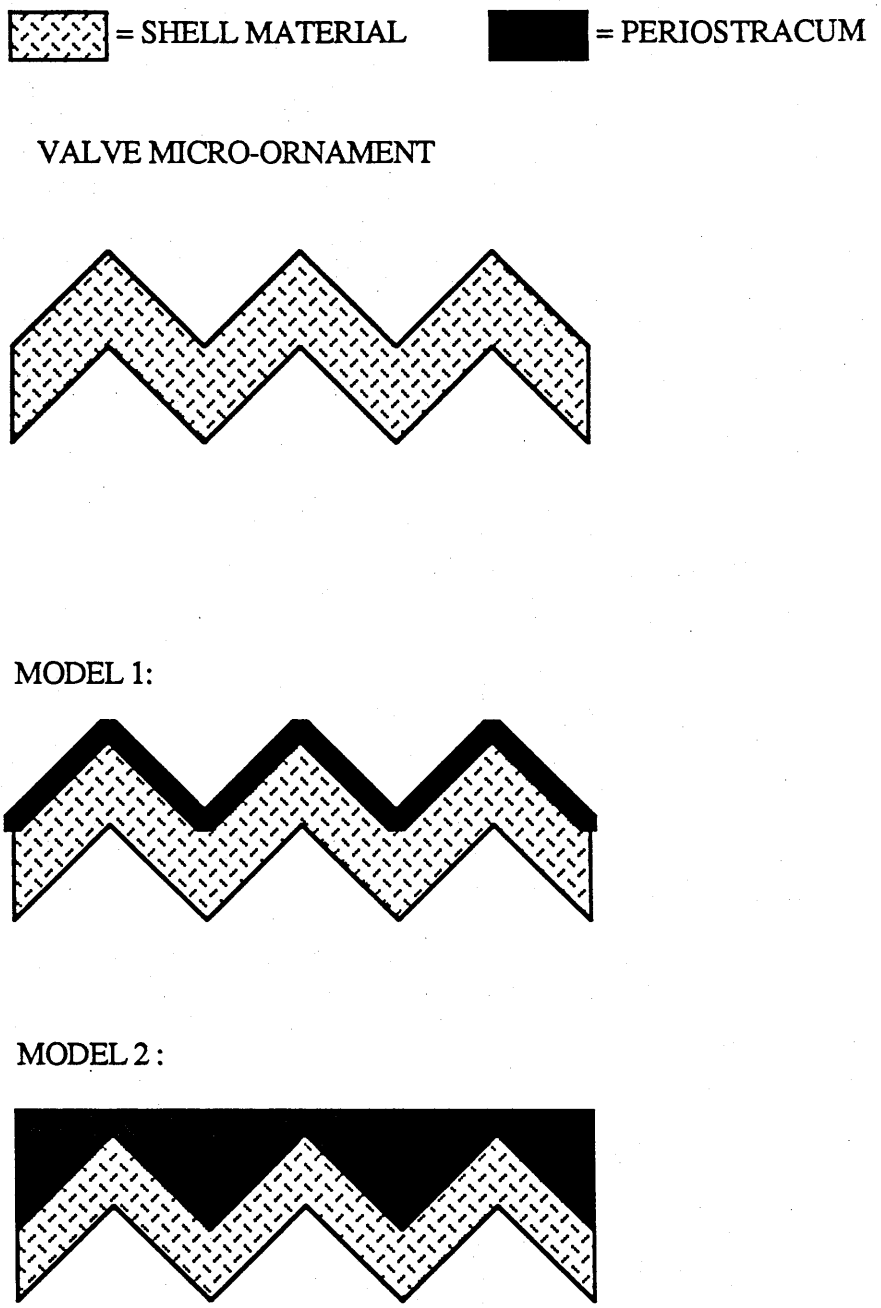


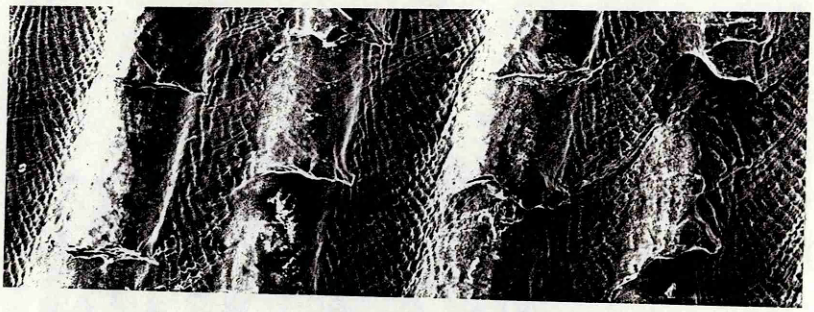
Figure 4.3: Hypothetical models of micro-ornament formation. For explanation see text below.

In Section 3.3.1.1, I argued that an infinitely flexible periostracum can only conform to substratal irregularities of width greater than twice the thickness of the periostracum. The same argument can be applied here. For a given thickness of periostracum there is a minimum wavelength of folding which can be achieved, and therefore a minimum scale of micro-ornament. How true is this? Scanning electron

microscopy studies were made of the micro-ornament of bivalves for which periostracal thickness had already been determined (Section 3.3.1.1). The same individual molluscs were used, in order that the exact periostracal thickness should be used, without the additional complication of intraspecific variation. Ventral valve margins were used so that direct comparisons could be made with the periostracal measurements. Although I am fairly certain that periostracal thickness is constant throughout ontogeny, micro-ornament on the 'just formed' shell was measured in order that direct comparison could be made with the previously measured thicknesses. Portions of shell were removed from the ventral valve margins and immersed in either concentrated sodium hypochlorite or potassium hydroxide solutions for 24 hours to remove all surface organic material. SEM of the gold sputtered valve surfaces was used to determine the finest scale of micro-ornament. Only features with a radial component were measured; care was taken to ensure that commarginal growth lines were not measured. Figure 4.4 illustrates a selection of those measured.

Figure 4.4: Scanning electron micrographs of valve external micro-ornament. (a) Shagreen micro-ornament of RV*Chlamys pusio*, Stub 0406, 8mm=100µm; (b) RV *Chlamys pusio*, stub 0222; (c) RV*Chlamys varia* , Stub 0400; (d) RV *Spondylus gaederopus*, Stub 0402; (e) RV *Corbula gibba*, Stub 0401.

a)



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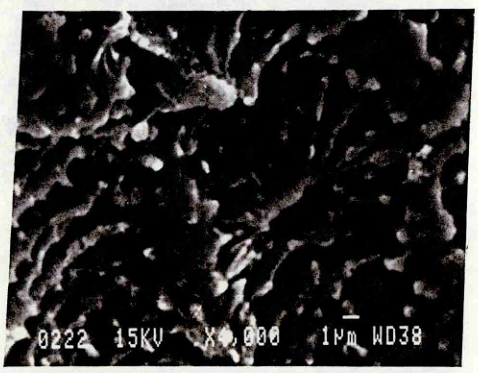

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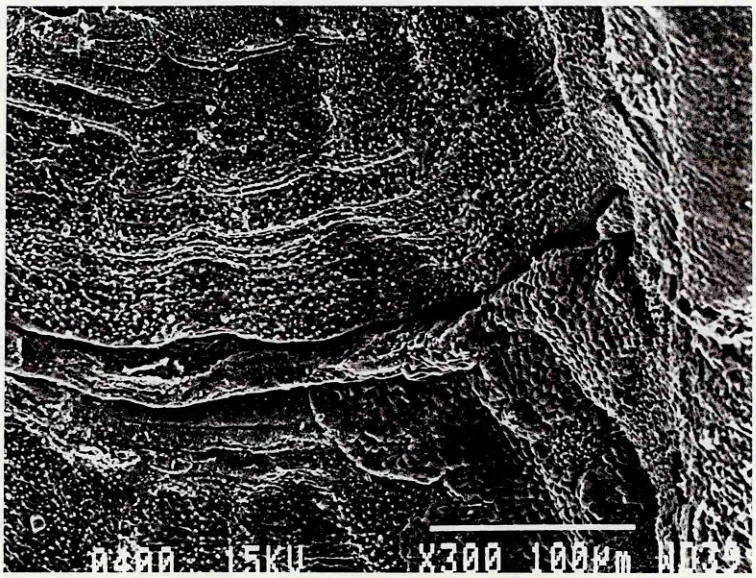

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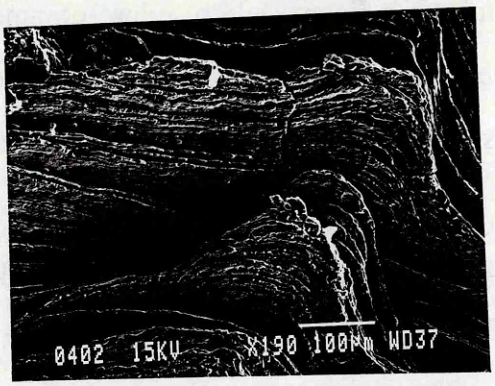
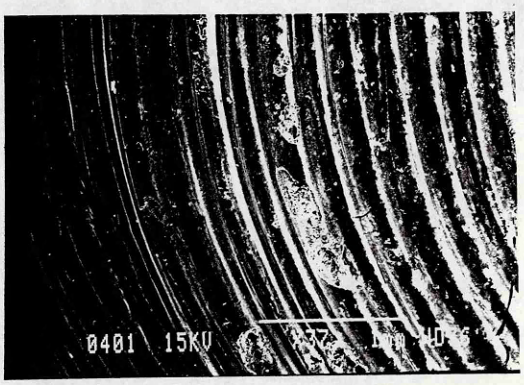


e)



Preliminary results have shown that bivalves with thick periostraca appear incapable of generating a fine micro-ornament. For example, *Mytilus edulis* (periostracal thickness 66μm), *Modiolus modiolus* (107μm), *Mya arenaria* (48μm) and *Corbula gibba* (146μm) display no radial micro-ornament. Those with periostraca, which do support radial microsculpture do so at a very coarse scale, e.g. *Aulacomya magellinanus* (156μm) is very coarsely ribbed, λ>1mm. By contrast bivalves with ultrathin periostraca are able to manufacture very fine micro-ornaments, e.g. *Lopha cristagalli* ~0.6μm and *Chlamys pusio* <1μm. Thus the basic premise is supported that only those bivalves with thin periostraca are capable of generating fine microsculpture.

Ideally, it should be possible to measure periostracum thickness and minimum micro-ornament scale for a large number of a range of living bivalves and plot these as a scatter graph. It should then be possible, by measuring micro-ornament on palaeontological specimens, to make reasonable suggestions as to their *maximum* periostracal thickness. How plausible is this?

This potentially rather exciting technique has, however, a number of complicating problems:

- Very fine microsculpture may not be preserved. For example Dhondt (1973) remarks upon how important shagreen micro-ornament is as a key to the generic recognition of *Chlamys*. However, she points out that in pre-Tertiary specimens this feature is seldom preserved. In such instances the finest ornament preserved may not correspond to the finest present in life; so leading to erroneous conclusions.

- The plotting of such data on a single graph assumes that all periostraca have the same flexibility and that this parameter has remained constant over evolutionary time. Undoubtedly this is an oversimplification.

- There is no guarantee that a periostracum will produce its finest possible microsculpture. Any data gained in this way must represent only the maximum possible thickness of periostracum.

Notwithstanding these criticisms I believe the technique offers at least some

information on this otherwise elusive parameter.

4.4.2 The mantle

For cementation to be possible, the periostracum must be laid onto the substrate surface. This is achieved by various modifications of the mantle. Figure 3.12 illustrates the accuracy with which the outer shell layer in *Crassostrea gigas* follows the microtopography of the substrate surface. Failure to achieve this high fidelity would result in a gap between the valve and the substrate too large to be occluded by cement. The role that the assumption of pleurothesis plays in this has already been discussed (Section 4.3.1). This requires a certain plasticity of the mantle, allowing it to drape across the surface of attachment. Waller (1990 and personal communication), in considering cementing pectinids, suggests that the onset of cementation must be heralded by a loss of mantle rigidity, possibly due to subcellular change such as reduction in the number of microtubules. These are reasonable suggestions but need to be checked by comparative TEM studies of mantle cells from cementing and non-cementing individuals. There has been no opportunity for such studies but these are envisaged for the future. Whatever the cause of changes in mantle rigidity, it is unlikely that anything other than the *most* exceptional of preservation will provide any direct evidence of its evolution in the fossil record.

4.4.2.1 Valve distortion and xenomorphism

However, perhaps an indication of mantle 'limpness' can be obtained from the ability of a bivalve to conform to an irregular substratum, i.e. by a study of valve distortion. Distortion of the 'lower' valve is not peculiar to cementing bivalves; other byssate pleurothetic taxa such as some non-cementing Pectinacea, also show this feature although the degree of conformity is much diminished. Distortion of the 'upper' valve, such that its morphology mimics that of the underlying substrate is more rarely found outside the cementing bivalves. First recognised by Stenzel, Krause and Twinning (1957) in Eocene anomiids and called allomorphic growth, the phenomenon

is now known as xenomorphism, a term coined by Stenzel (1971). The superb detail produced by some xenomorphic bivalves such as oysters has tremendous potential for the investigation of perishable or diagenetically unstable substrates. For example, Lewy (1972) has used oyster xenomorphic ornament to determine details of ammonite shells, whilst Rohr and Boucot (1988) describe a possible plant from xenomorphism of Cretaceous oysters from Brazil.

Xenomorphism is an obvious consequence of a bivalve growing across an irregular substratum. If the 'lower' valve encounters a topographic high then its elevation to cross that obstruction must be accompanied by an equal raising of the 'upper' valve in order to conserve body space. During the course of this study it has been apparent that certain cementing bivalves are capable of high fidelity xenomorphism, e.g. Ostreacea, Anomiacea and Myochamidae, while others e.g. pectinids and spondylids provide only the fuzziest details of their substrates.

Fidelity of xenomorphism is, I believe, inversely correlated with thickness of mantle margin, or more specifically with the development of the middle lobe. Those bivalves which are capable of precise xenomorphism have only poorly developed middle lobes, with only one or two rows of sensory tentacles and no ocelli (see *Ostrea edulis* Figure 3.5(a)). By contrast the pectinids and spondylids (see Figure 3.5 (E,G,H)), have thickened middle lobes, densely packed with tentacles and ocelli. Substrate topography is translated to the 'upper' mantle by its resting on the 'lower' and it is the outer fold which is responsible for the actual process of shell secretion. Whether or not minor topographic changes are taken up by the 'upper' valve will depend on the degree to which the 'lower' mantle can effect the'upper'. Where the signal has to pass through a two layer thickness of sensory organs that signal will be very diffuse.

4.4.2.2 Mantle extensibility

An important requirement for cementation is that the periostracum should be applied directly on to the substrate, extending the extrapallial cavity so that shell material is

added to the periostracum and not just to the valve margins. Tank observations on living cementers (*Chama, Ostrea edulis, Crassostrea gigas, Spondylus gaederopus* and *Chlamys pusio*) showed that all, during normal activity, were able to extend their mantle margins far beyond the valve edges. Such activity extends the extrapallial cavity ventrally, exposing large expanses of free periostracum. This behaviour contrasts sharply with that of many non-cementing bivalves whose mantle margins protrude scarcely further than the valve edges (see Figure 4.5).

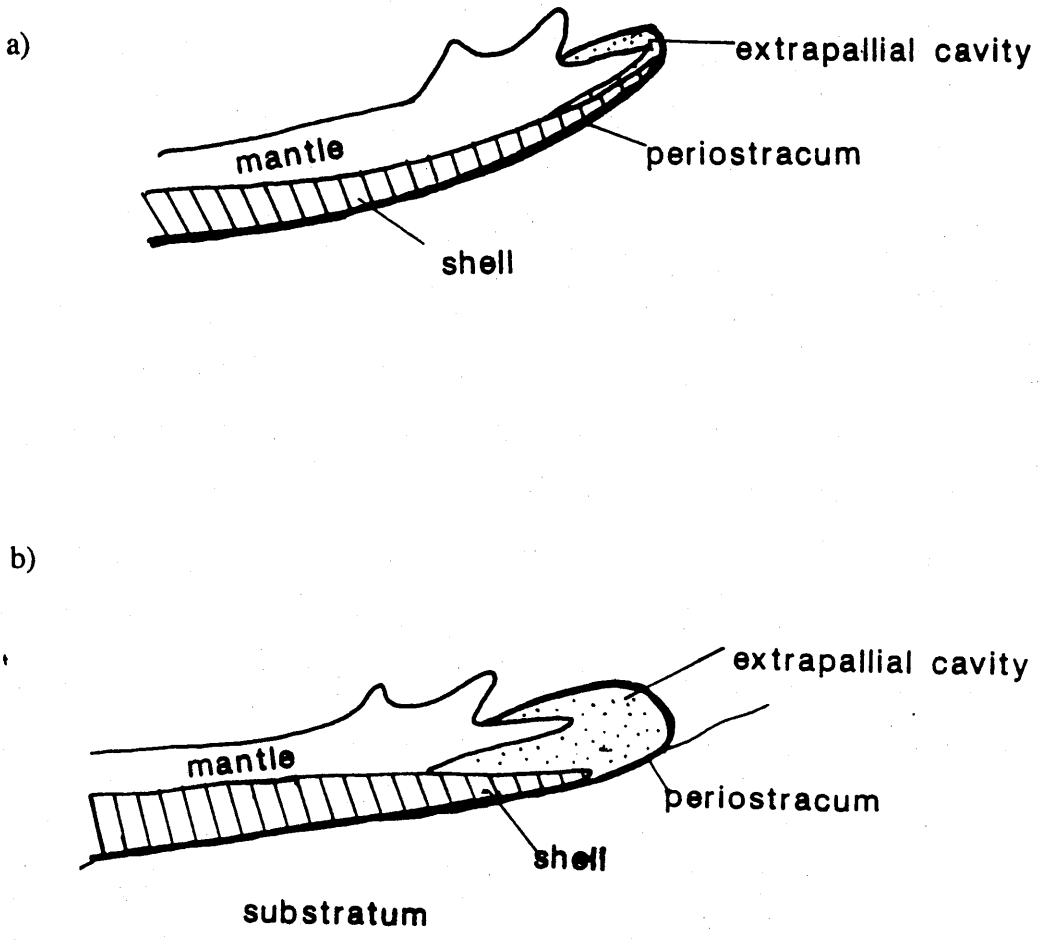


Figure 4.5: Arangement of the mantle edges in normal gaping activity in (a) non-cementing bivalves and (b) cementing bivalves.

Searches were made to find morphological differences to account for this variation in extensibility in mantles. Scanning electron microscopy failed to find any differences

in gross mantle morphology or arrangement of muscle fibres. Basic differences were noticed, however, in the positioning of the points of mantle attachment to the valve, i.e. location of the pallial myostraca. The effect of this may be demonstrated in live *Mytilus* and *Ostrea*. Stimulation of the mantle edges with a sharp needle causes them to be drawn back from the valve margins. In the case of *Mytilus* this withdrawal is minimal, only as far as the pallial line, whilst *Ostrea* mantle retracts half the valve height to the site of muscle insertion. The amount of contraction is limited by the positioning of the pallial attachment. The Ostreidae lack any discernible pallial line. Indeed dissection shows no sign of adhesion of the mantle to the valve except at the adductor myostracum and shell microstructure studies have revealed no pallial myostraca.

Quantification of positioning of pallial attachment.

Casual inspection reveals that the pallial attachment varies greatly within the Bivalvia, but that in the cementing bivalves it is consistently more dorsally placed. There is no precedent in the literature for quantifying the position of pallial attachment, yet it would seem to be a useful parameter to record. Descriptive terms scattered through the literature, such as 'withdrawn' and 'close to the valve margins', are vague and only relative.

There is a general problem with interspecific comparisons because of the enormous variation in valve convexity. Accordingly, it was decided to quantify the positioning of pallial attachment by recording the ratio of the length of mantle outside the pallial line to the total length of the mantle. The method is illustrated in Figure 4.6. Inset ratio (IR) values close to zero indicate pallial attachment on the ventral valve edge, whereas values of 1 indicate a point at the umbo. (Initial attempts to measure IR utilised the linear dimensions of valve height and height to pallial attachment, thus failing to take account of the curvature of the valve. Clearly this prevents comparisons between taxa.)

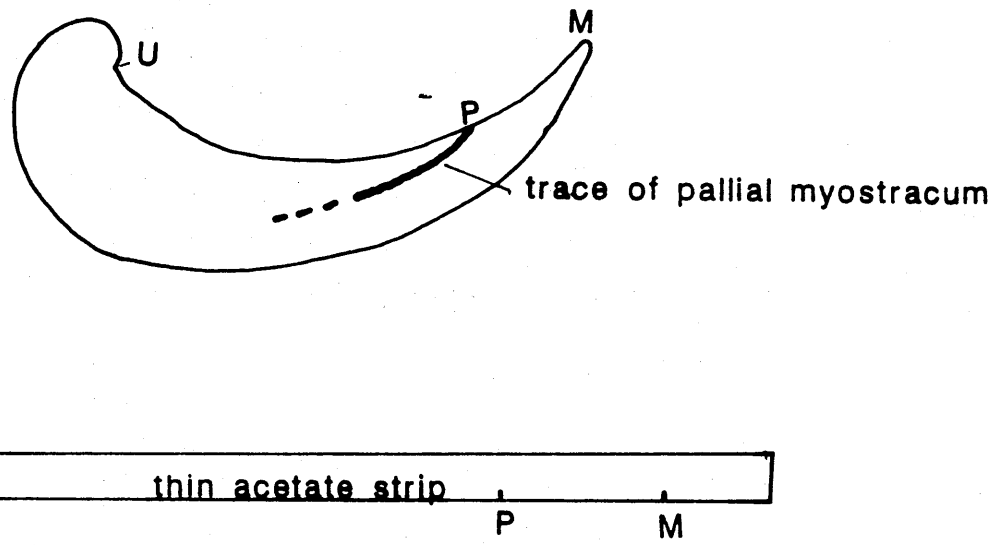


Figure 4.6: Diagramatic illustration of the method used to determine IR. The inset pallial attachment is measured by using the narrow strips of thin acetate film, tapered at one end. The tapered end of the strip is placed inside the umbonal cavity and allowed to drape along the height, following the curvature of the valve. The position of pallial attachment (P) and the ventral valve margins (M) are then marked on the film. Linear measurements of PM and UM, in millimetres, are then used to derive IR by the formula: IR=PM/UM.

Measurements were made by recording the relative positions of the umbo, pallial attachment and ventral valve edge on narrow strips of very thin acetate film. This method is clearly not ideal; in the future these data might be gathered by digitization and subjected to image analysis. However, the approach used here does have redeeming features. For example, the method is rapid, producing with practice consistent values which can also be applied to palaeontological material, including internal moulds.

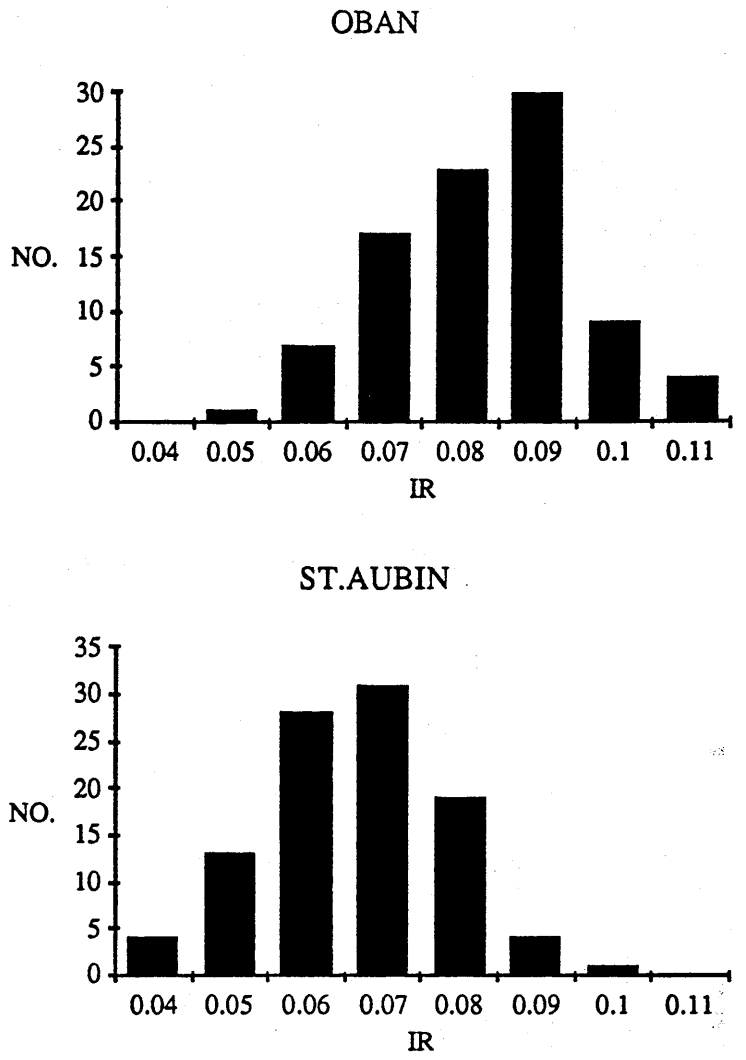


Figure 4.7: Frequency histograms of the intraspecific variation in IR values recorded from *Mytilus edulis* collected from Dunstaffnage Bay, Oban (N=96) and St Aubin-sur-Mer, Normandy (N=100). Only right valves were utilised. Student's t-test shows that there is no significant statistical difference in means between these two distributions at the 10% level.

Pilot studies on individuals of *Mytilus edulis* assessed the intraspecific variability of IR (see Figure 4.7). Measurements of 96 specimens collected in Dunstaffnage Bay, Oban produced a mean IR value of 0.08, with a standard deviation ($\sigma n-1$) of 0.01. 100 conspecifics, collected at St. Aubin sur Mer in Normandy had a mean IR of 0.07 ($\sigma n-1=0.01$). Analysis of these two data sets by Student's t-test, as described by Siegel (1956), shows that there is no significant difference between the the means of the distributions at the 10% level.

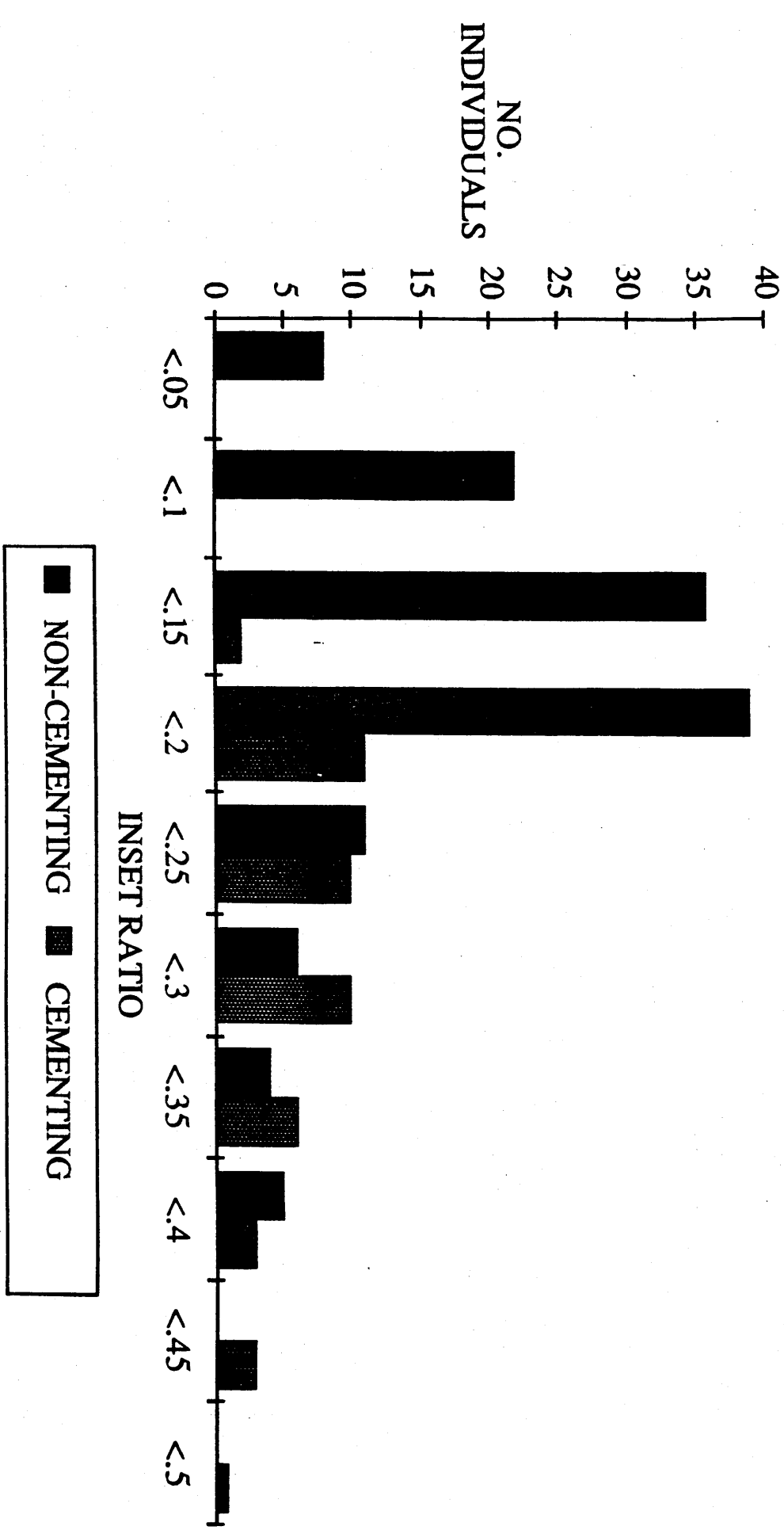


Figure 4.8: Frequency of IR distribution from a wide range of bivalve species. Species means plotted, from data displayed in Appendix 3.

Inset Ratios were measured for nearly two hundred species of modern cementing and non-cementing bivalves, spread over a wide range of taxa, using specimens from the NHZ and my own collections. These data are presented in Appendix 3. The IR recorded for these taxa exhibit a wide range of values, from *Lithophaga nigra* (0.03) to *Ostrea edulis* (0.49).

The data illustrate only the range of IR within the class. There have been notable omissions to this study, including the Trigoniacea, Leptonacea and Mactracea, whilst there has been an over concentration on mytilaceans and pectinaceans. Without measuring a large number of individuals of representatives of every bivalve taxon it is impossible to give any quantitative analysis of IR variation. Figure 4.8 displays as a frequency histogram the mean IR values for all species measured. I suspect that the true range of IR distribution for the Bivalvia will be positively skewed, due to low values for relatively abundant taxa such as venerids, tellins, arcs, ericynids. Figure 4.8 does show that the cementing bivalves have values which fall in the higher part of the range, i.e. that they have a more dorsal pallial attachment. Even amongst the Unionidae of West Africa there is a statistically significant difference in the IR values between the cementing etheriids and the non-cementing forms such as *Cameronia,* and *Spatha* (see Figure 4.9).

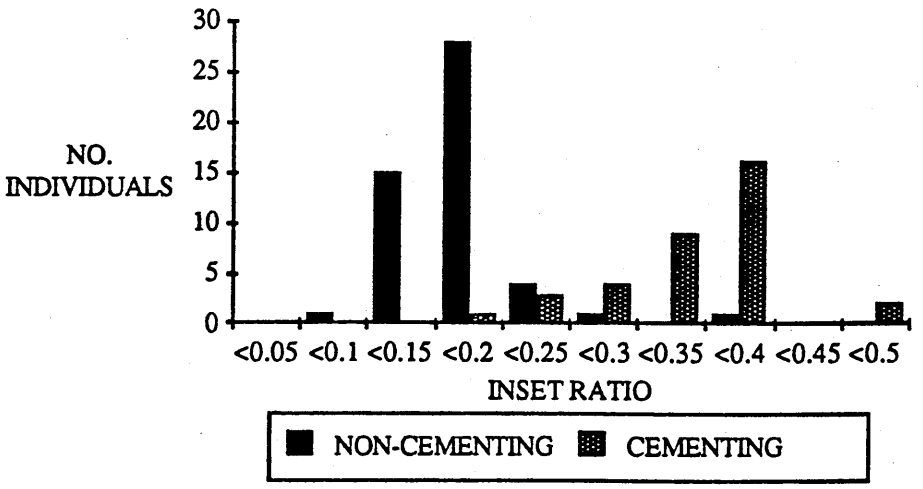


Figure 4.9: Distribution of IR values for members of the Unionidae from W. Africa, N=82. The cementing taxa have, in general, higher IR values than the non-cementing taxa. Student's t-test shows the difference in means to be significant at the 5% level. Specimens from NHZ. Data from Appendix 3.

How does inset pallial attachment relate to mantle extensibility?

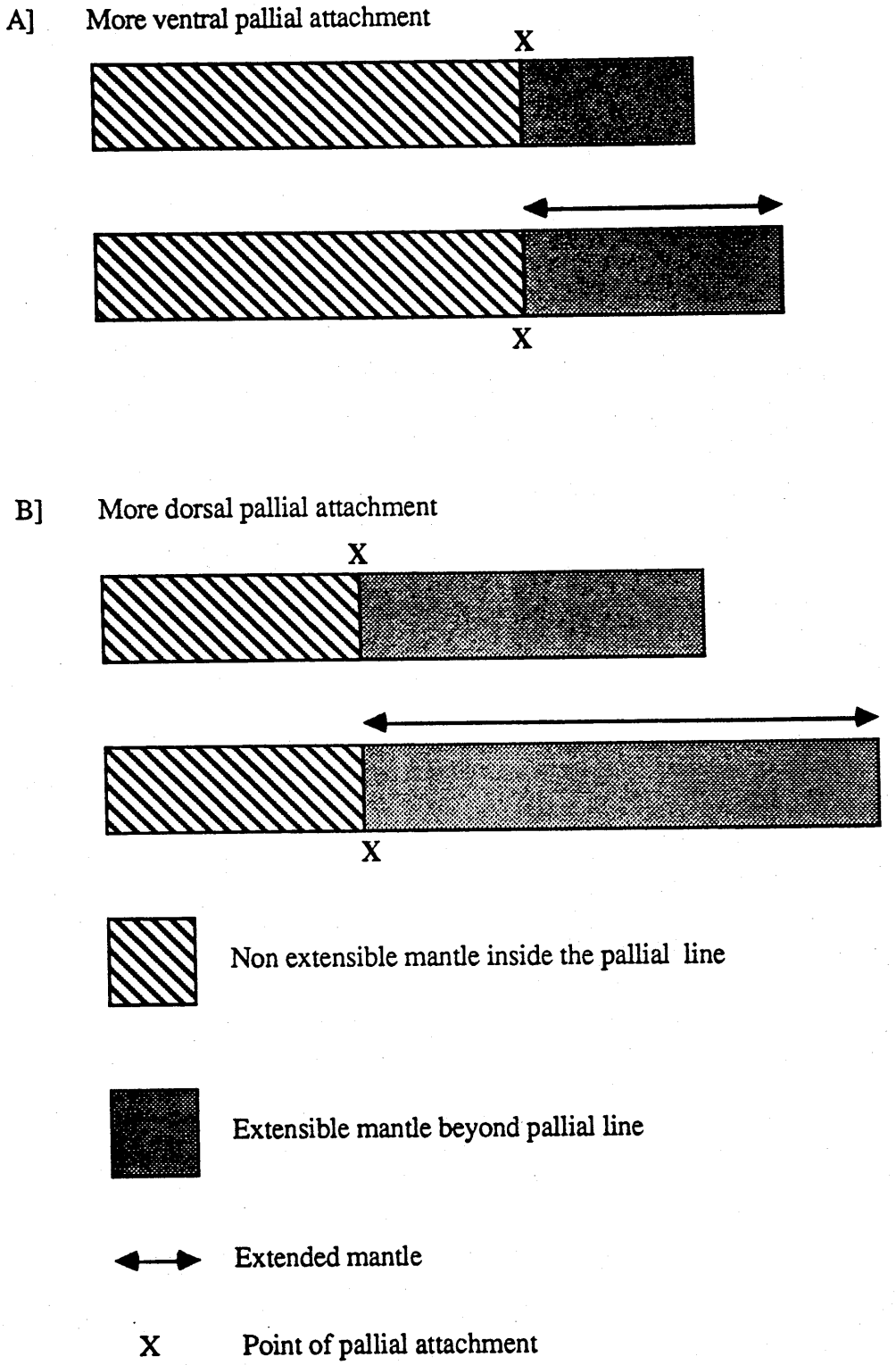


Figure 4.10: Relationship between inset of pallial attachment and mantle extensibility.

The argument has been presented that cementing bivalves require a highly extensible

mantle margin in order to cement and it has been shown above that the pallial attachment in such species is typically dorsally inset. Are the two observations related?

Consider two hypothetical mantle margins identical in all but the positioning of the pallial line, illustrated in Figure 4.10. Mantle A represents a generalised non-cementing bivalve, with a less inset pallial line, whilst Mantle B, with a more inset pallial line, represents a cementing bivalve. Applying an arbitrary extension of 50% to the free mantle, outside the pallial line, clearly shows that Mantle B is capable of greater extension.

Functional significance of an inset mantle?

Possession of a highly inset pallial line is not confined to the cementing bivalves. High values have also been recorded in non-cementing Pectinacea, Limopsacea, Anomiacea and Arcticacea. Kauffman (in Moore, 1969) argues that this is a characteristic feature of epifaunal bivalves. However, the Mytilacea and Arcacea are obvious and important exceptions to this in having low IR values. Dorsally inset pallial attachment may be regarded as a functional necessity in narrow bivalves. These 'flatter' forms require more space to withdraw the mantle margins than do more globose morphologies. Since most of the pleurothetic bivalves are fairly flat they would seem to be preadapted in this respect.

It also would seem that an inset pallial line is simply a functional necessity for those bivalves with well developed middle mantle folds with copious tentacles and ocelli. In order fully to close the valves, for example during adverse environmental conditions or evasion of a predation attempt, the mantle must be fully withdrawn. In taxa with particularly well developed mantle margins this necessitates bringing them back further into the wider part of the valves, i.e. more dorsally.

Preadaptation or adaptation?

Theoretically one should be able to follow changes in the positioning of the pallial line over geological time. It should be thus possible to determine whether a dorsally inset

pallial line and highly extensible mantle margin was a preadaptation for cementation, or whether the feature is an adaptation to the habit.

Perhaps the most obvious subjects for this study are the oysters, with their long evolutionary history and predominantly calcitic shell, providing a complete fossil record of the inner surfaces. However the lack of a true pallial line poses problems; although it is demonstrable that the modern oysters have no mantle attachment except at the adductor, it is difficult to verify that this is the case in fossil material. It is also well known that during the course of evolution in the Ostreidae the adductor gradually shifted ventrally, which Stenzel (1971) attributes to increasing efficiency of muscle leverage. Such unrelated evolutionary changes may complicate the issue. For these reasons members of the Hippuritacea, Spondylidae and Plicatulidae were chosen instead for this study.

(i) Hippuritacea

Extinct clades of cementing bivalve also have dorsally inset pallial attachment. Apparently the rudists, like the oysters, lacked a true pallial line (Skelton, personal communication), mantle attachment being confined, rather, to isolated patches of myostraca. Acetate peels of their ancestors, the megalodontids, were examined in NHP. Peels taken from specimens of *Pachymegalodon crassus* from the Lias near Verona (L87691-4) clearly show the linear trace of a pallial myostracum indicating their possession of a pallial line. The subsequent loss of this pallial line may have been a vital feature of the evolution of the cemented habit in the rudists. Further studies are required to look at the very earliest rudists to determine whether this loss heralded cementation or whether it was an early adaptation to the habit.

(ii) Spondylidae and Plicatulacea

The Spondylidae and Plicatulacea both have the advantages to this study of being monogeneric clades, but even here there are problems. In both, the pallial myostraca lie within the aragonitic inner shell layers and hence any diagenetic loss or recrystallisation of that aragonite will destroy the evidence. For example in the Spondylidae this factor severely limits Mesozoic IR measurement. Of 663 Campanian

Spondylus studied from the Ivö Klack deposit in Sweden (held in DCM) only 4 specimens (<0.1%) preserved traces of the pallial line.

IR values were collected for fossil and Recent material (*Plicatula* N=67 and *Spondylus* N=83) in the following institutions: NHZ, NHP, DCM and SD; data are recorded in Part II of Appendix 3. These results are recorded in Figure 4.11, which plots IR value against age. Mindful that species identification in museum collections is not necessarily correct, the data have been plotted for every specimen measured rather than attempting to calculate species means.

Figure 4.11(a) shows the results obtained for the Spondylidae. No significant change is recorded over geological time (however, it should be noted that I have no data for the very earliest members of the clade): the pallial attachment is consistently dorsally inset. This is not entirely surprising; the Spondylidae are members of the superfamily Pectinacea which are characterised by this feature. In this respect the family may be said to be preadapted to cementation. Newell (1937) remarks that the pallial line in "Palaeozoic pectinoids is relatively closer to the margins than in modern Pectinidae". Nevertheless his figures show that they are well inset. Newell suggested that the difference was due to a development of the middle mantle lobe.

The results for the Plicatulidae (Figure 4.11(b)) are somewhat unexpected. The IR values for modern *Plicatula* are not particularly high when compared to other cementing bivalves. Yet fossil IR values appear higher. The data are well scattered but it is possible to perceive a decrease in IR over geological time i.e. a shift towards the ventral valve margins. This is rather the reverse trend to that which might be expected *were* an inset pallial line to correlate with mantle extensibility. One problem is that, in general, plicatulids cement for only a short time and at the moment it is unclear whether the positioning of the pallial line varies over ontogeny.

The evolution of pallial attachment positioning is likely to follow different patterns in each of the clades of cementing bivalves. Even in the three clades considered here the response appears to be different; in the rudists evolution of cementation may be linked to a loss of a pallial line, in the Spondylidae there is no apparent shift in the

positioning of pallial attachment, whilst in the Plicatulacea the trend appears to be towards a more ventral attachment.

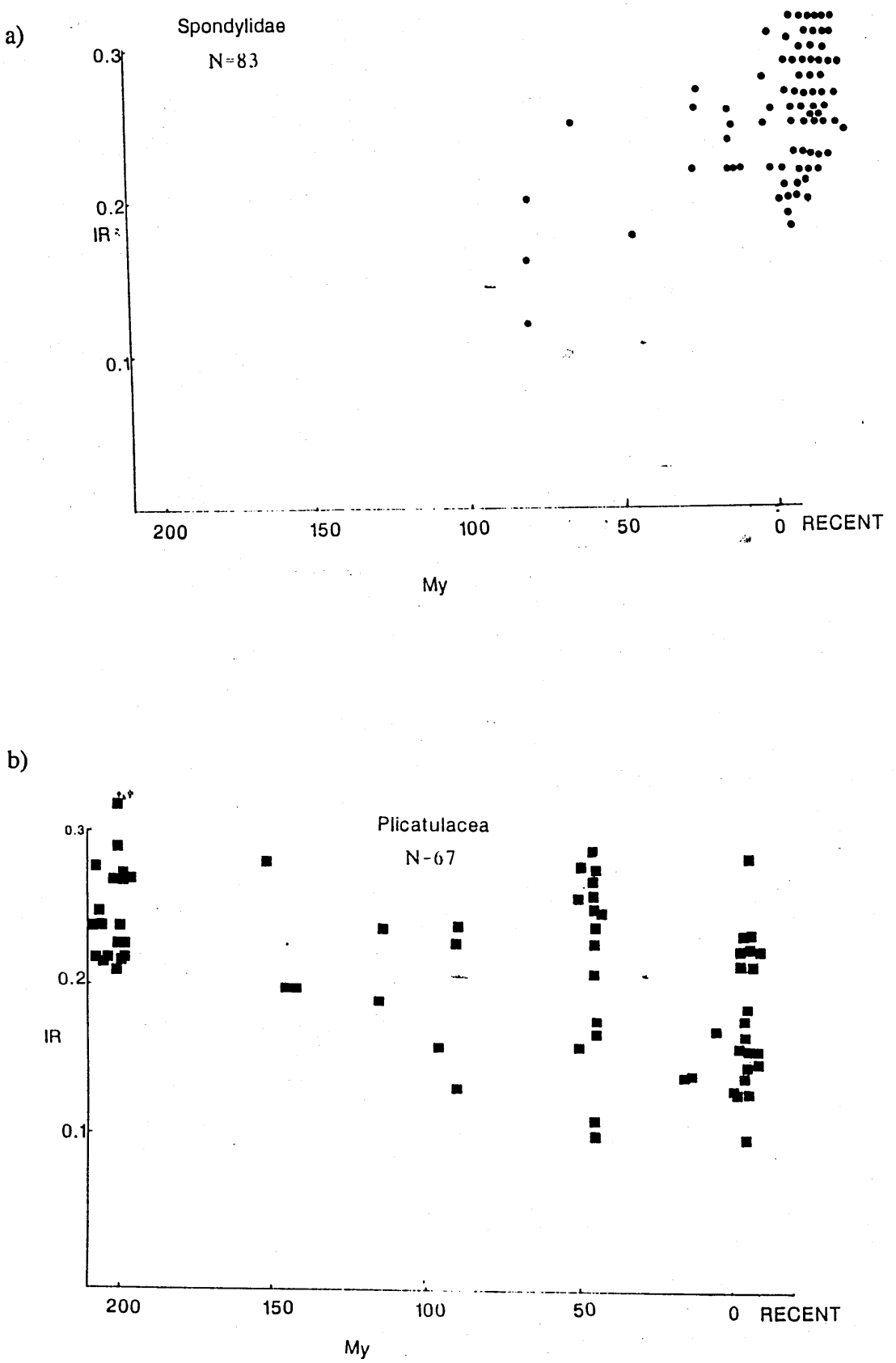


Figure 4.11: IR measurements plotted over geological time. Data from Appendix 3. (a) Spondylidae, and (b) Plicatulacea.

4.4.3 Cementation by flanges or spines

In some clades spines or flanges may be utilised to effect attachment (see Figure 4.12). These have been observed in all cementing pectinids, Spondylidae, some Plicatulidae, *Etheria*, most *Chama*, some rudists e.g. certain Requieniidae have flanges(see Skelton and Gili, in press), whilst the Radiolitidae have both spines and flanges, and certain oysters e.g. *Lopha cristagali*. Clades which appear unable to produce these valve outgrowths include the Pseudomonotidae, Terquemiidae, Dimyidae, Cleidothaeridae and Myochamidae.

a) b)

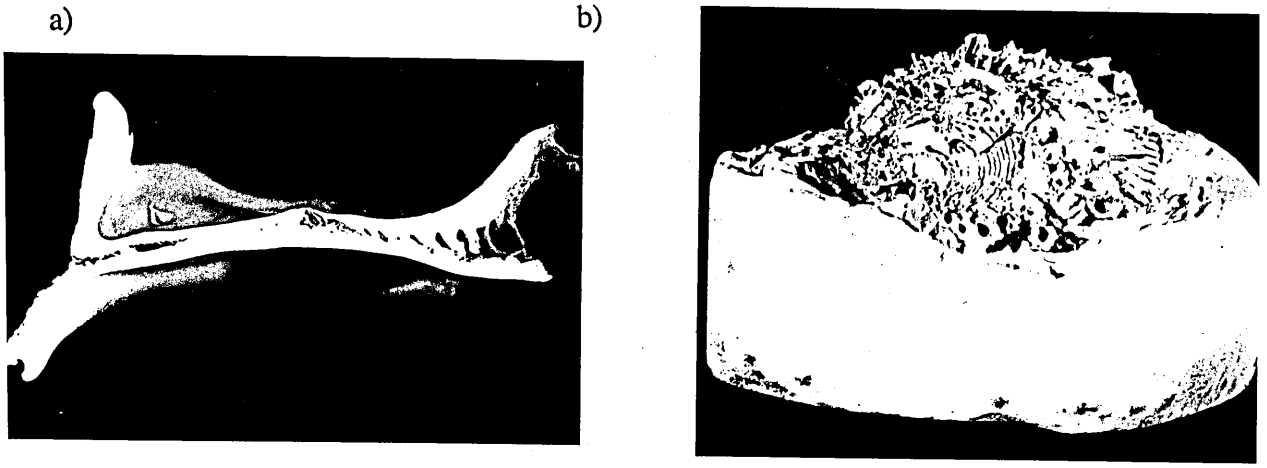


Figure 4.12: Use of spines and flanges in the cementation of the Spondylidae. (a) Recent *Spondylus gaederopus* attached to a conspecific, valve height =52mm, and (b) base of RV of *Spondylus dutempleanus* (Upper Maastrichtian - Stevns Klint, Denmark). Attachment area =24mm. Prepared by Sten Jakobssen (DCM).

Logan (1974) makes a careful functional study of the spines of the spondylid, *Spondylus americanus*. He lists six possible functions for the spines:

1) Supports for sensory mantle outposts, as postulated by Rudwick (1965) for the brachiopod *Acanthothyris*.

2) Promoting the growth of camouflaging algae.

3) Discouraging the attachment of fouling epibionts.

4) Protection of the soft parts by guarding the ventral gape.

5) Attachment to a hard substrate.

6) Anchorage in soft sediments.

Of these, Logan favours a primary function of protection of the soft parts, with

secondary encouragement of settlement of camouflaging epibionts, a function also discussed by Vance (1978) and Feifarek (1987). He specifically rejects the attachment to the substrate because the spines do not appear rhizoid. Yet my observations show that the spines of *Spondylus* do attach to the substrate. Undoubtedly the long pointed spines on both valves which curve towards the ventral valve margins are antipredatory. But Logan virtually ignored the downward pointing spines on the right valve. Three alternative functions are now suggested for these spines:

1) Provision of anchorage in soft shifting sediments. This function has been suggested for the long tapering spines in the non-cementing Chalk *Spondylus spinosus*.

2) Acting as supports to raise the ventral valve margins clear from the substratum after the cessation of cementation. In this case there is *no* attachment of these spines to the surface.

3) These spines are actually capable of adherence and are therefore an important part of the cementation strategy.

Most spondylids do not live in soft sediments. Rather they inhabit clean, hard substrates and therefore hypothetical function 1 is rejected, as a general explanation. Inspection of Recent specimens of *Spondylus* shows that these valve outgrowths are attached to the substrate and not resting merely resting upon it. For this reason the third possible function is favoured over the second, although it is acknowledged that the role of these spines and flanges may also include lifting of the valve margins.

The ability to form such spines and flanges is linked to the mantle extensibilty discussed in the previous section. In order that shell material can be deposited at the tip of the growing flange the mantle must be extended far beyond the valve margins. Indeed in certain specimens of spinose *Chama*, e.g. *C. lazarus*, which has spines at the valve margin, i.e. forming at the time of death, the pallial line is seen to be dorsally deflected opposite the outgrowth. Just as the pallial line of certain burrowing taxa is inflected to form a pallial sinus to accommodate the retracted siphons, this inset in *Chama* may be interpreted as providing space for the mantle required to secrete the

spines.

It should be possible to chart the use of spines in attachment in the fossil record. Inspection of spondylid material of all ages shows that flangous outgrowths have been intimately involved with cementation throughout their geological history. Indeed the oldest specimens known to me, *Spondylus consobrinus*, collected from the Bajocian of Normandy, (specimens NOR005) shows clear attached flanges on the right valve. Very few specimens genuinely lack spines or flanges on the right valve, although the Recent *Spondylus pacificus* is one such example. Inspection of Zavarei's monograph (1973) on the post-Jurassic spondylids reveals that the number of spineless spondylids has always been low.

Inspection of Chamacea in the collections in NHP and NHZ suggests that Recent members of this superfamily possess more spines and flanges than fossil examples. Clearly, it is necessary to find a way of quantifying spinosity.

4.4.4. Valve edge profiles

Observations of living bivalves, recorded in Section 4.4.2.2, imply that the cementing bivalves are able to extend the extrapallial cavity ventrally during normal valve growth. The form of the valve margins may be used to gain information about how the mantle edges are applied to the substratum.

Comparisons of the morphology of the valve margins of various cementing and non-cementing bivalves have been made. Individuals with pristine edges, free from marginal damage were selected. These valves were ground down, with carborundum powder, to produce sections along the plane of the valve height. These were then examined with a binocular microscope and the camera lucida attachment was used in order that the valve margin profiles could be drawn for comparison. Figure 4.13 illustrates a selection of the drawings made.

All the cementing bivalves examined showed valve margins which curved asymptotically towards the substratum. This is very clearly illustrated by the rudists, see Figure 4.14. By contrast, the non-cementing bivalves display margins with a

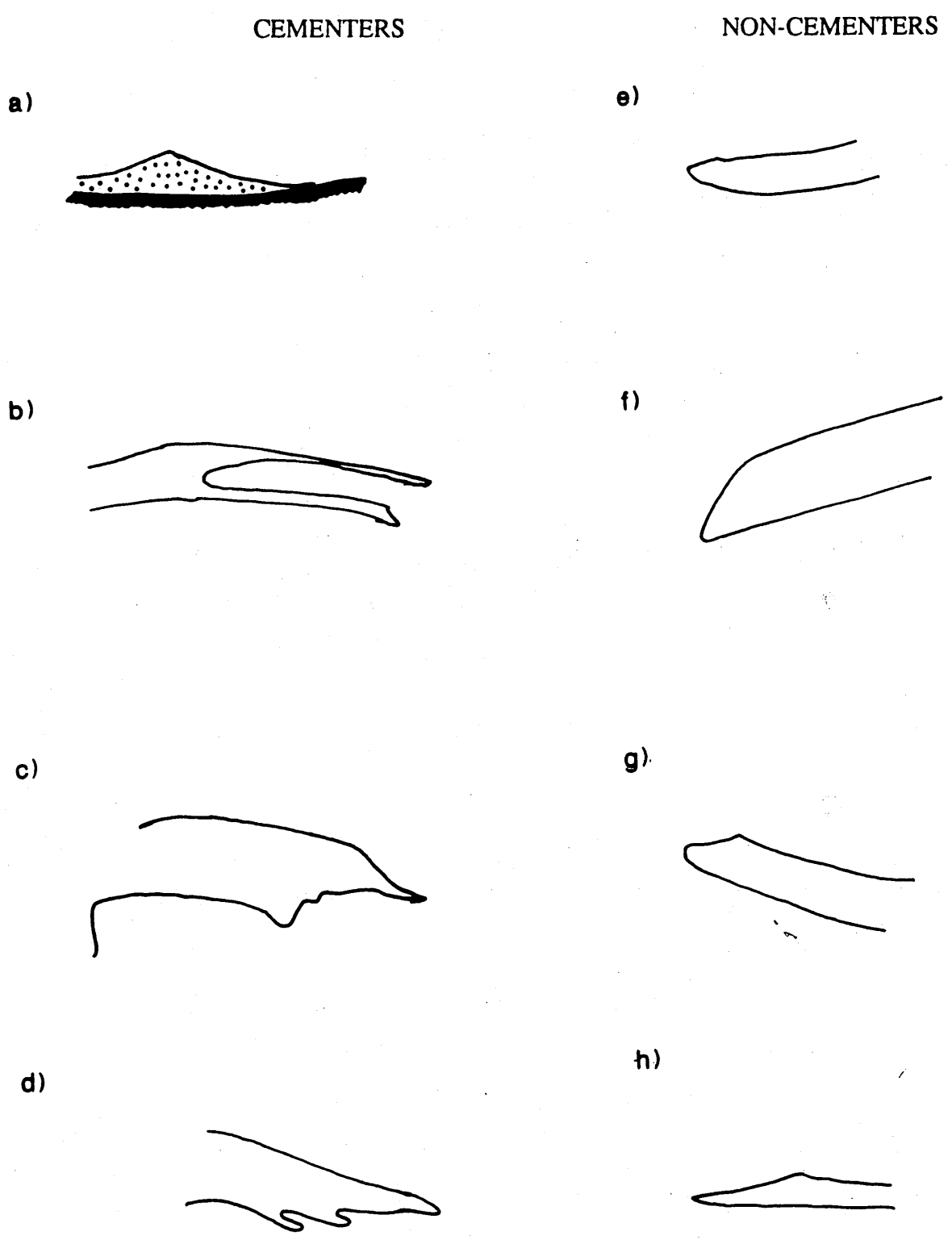


Figure 4.13: Ventral valve edge morphology of cementing and non-cementing bivalves, drawn from camera lucida views of valves ground down along the plane of valve height. (a) *Crassostrea gigas* (6 week spat attached to glass), X25; (b) *Crassostrea angulata*, X5; (c) *Spondylus butleri*, X6; (d) *'Chama'*, X6; (e) *Mytilus edulis*, X6; (f) *Mercenaria mercenari*, X6; (g) *Cerastoderma edule*, X6 and (h) *Chlamys opercularis*, X6. For all cementing bivalves records are for the cemented valve, for all others the right.

steeper termination.

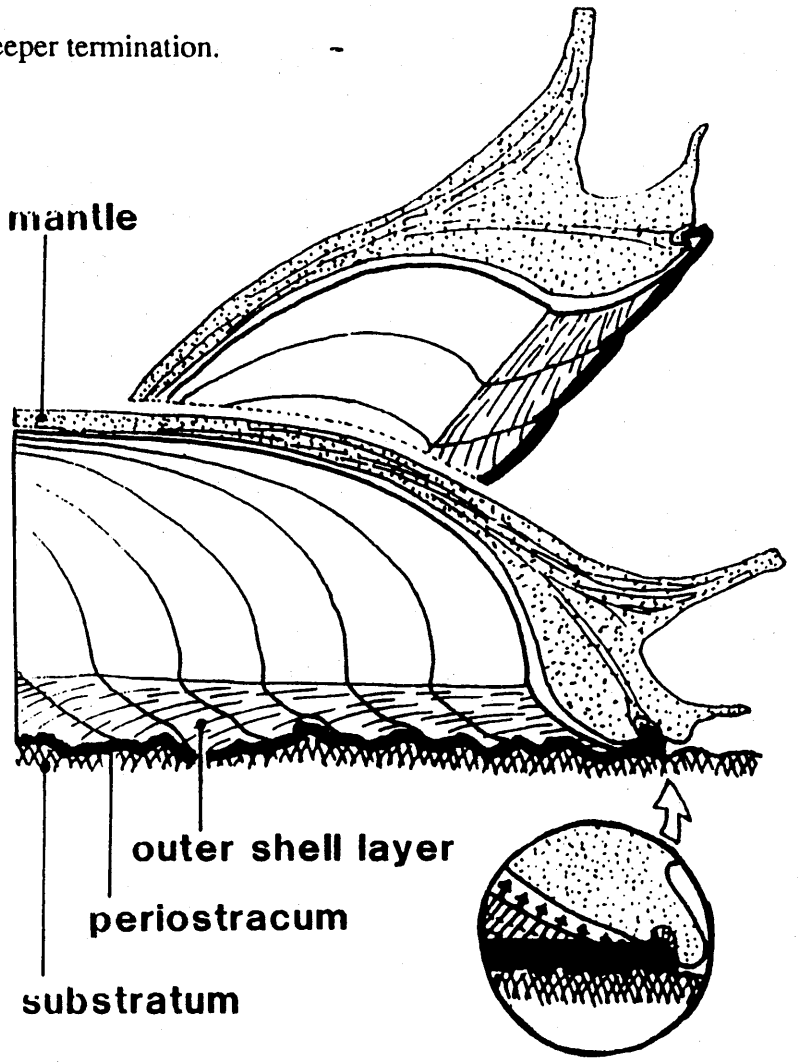


Figure 4.14: Growth line patterns in the anterior margins of the attached valve of a generalised encrusting rudist. From Skelton (unpublished).

This 'runway-like' profile is a consequence of the periostracum being laid down flush against the substratum and shell material being added to the free periostracum over a broad area rather than being accreted onto a very narrow zone of preformed shell. This gives more opportunity for extrapallial fluid to leak through the periostracum.

Figure 4.15 is an electron micrograph illustrating the valve edge of an Upper Chalk *Spondylus latus* attached to an echinoid test. A thin veneer of shell material is clearly visible extending ventrally, reinforcing the argument that shell material is not merely accreted to the very valve edge but rather to a broader expanse. Minor bumps are apparent in this layer of newly formed shell, and are interpreted as caused by overgrowth of the tubercles of the echinoid.

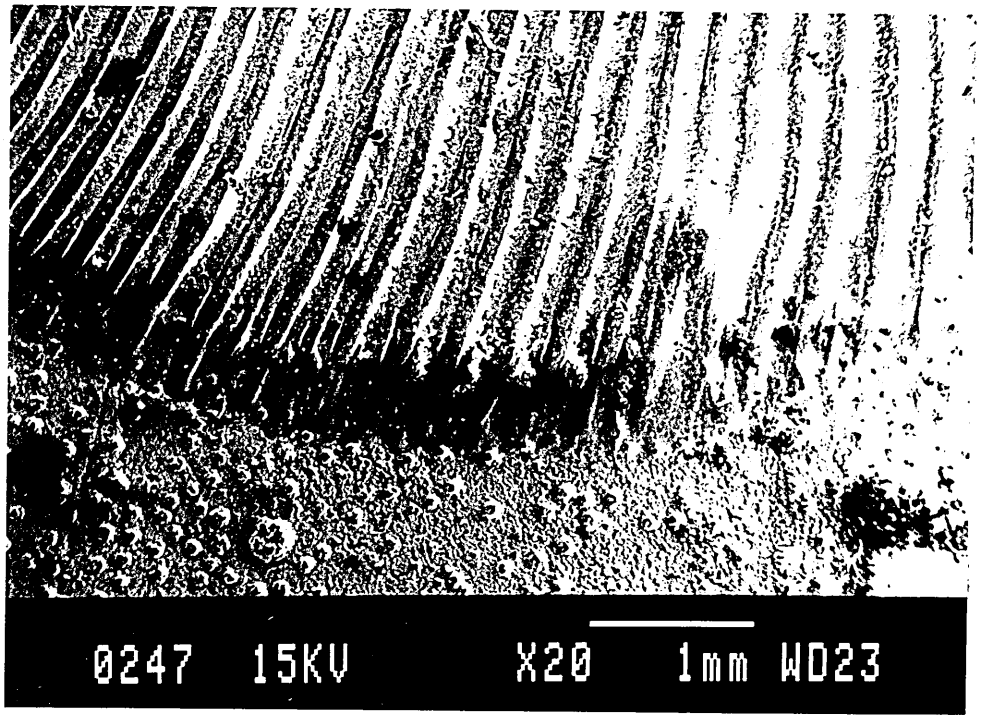


Figure 4.15: Electron micrograph of the ventral valve margins of *Spondylus latus* attached to an echinoid test, Stub EMH0247, ex Blackmoor Collection (NHP) collected from the Upper Chalk around Salisbury. Echinoid tubercles visible through the advancing *Spondylus* valve.

Observations on individuals of *Ostrea edulis* and *Crassostrea gigas* held in aquaria at the Open University reveals marginal valve growth may be very rapid. A very thin prismatic layer is deposited way in advance of the rest of the valve so that a clearly identifiable flange 5-10mm may be observed. This flange of shell material is very flexible and has been observed to alter its attitude over a period of days. Presumably the leading edge of this flange is constantly attached to the periostracum and therefore subsequent movements in the mantle can affect its positioning. Removal of this prismatic flange led to the oyster rapidly replacing it at rates of up to 2-3mm per day. Potential exists for following the evolution of valve margin profile in palaeontological material by studying growth lines, but has not been attempted here.

4.5 ENVIRONONMENTAL CHANGES AND CONSTRAINTS

Changed environmental conditions may facilitate the onset of cementation in certain groups already constructionally preadapted.

4.5.1 A relationship between the evolution of cementation and seawater geochemistry?

Sandberg (1983) described an oscillating trend in the mineralogy of abiotic carbonates during the Phanerozoic. He identified alternating 'aragonite inhibiting' and 'aragonite facilitating' phases of seawater chemistry which resulted in the primary precipitation of calcite and aragonite (with high magnesium calcite) respectively. 'Aragonite inhibiting phases' existed during the Cambrian to the late Carboniferous and the late Triassic/early Jurassic to the mid Cainozoic. Sandberg postulated that these changes were related to oscillating partial pressures of carbon dioxide in the atmosphere leading to changes in the carbonate ion concentration in the oceans. Subsequent work by Wilkinson, Owen and Caroll (1986), Wilkinson and Given (1985), Railsback and Anderson (1987) and Opdyke and Wilkinson (1990) have explored the links which may exist between changing seawater chemistry and hydrothermal weathering, eustasy and sealevel regressions and transgressions.

There may be an interesting tie between Sandberg's observations and the evolution of the cemented habit if the assumption made in Section 3.3.2.3, that the mineralogy of the cement is the same as the outer shell layer, is correct. It is the timing of the evolution of the habit in relation to the aragonite inhibiting and the aragonite facilitating phases which is interesting. Table 4.3 gives the mineralogy of the outer shell layer of each clade along with their first appearance data.

CALCITE OUTER SHELL	ARAGONITE OUTER SHELL
Pseudomonotidae (early Carboniferous)	Etheriidae (Pliocene)
Chlamys pusio (Recent)	Chamacea (late Cretaceous)
Eopecten (middle Jurassic)	Cleidothaeridae (Miocene)
Hinnites (Miocene)	Myochamidae (Miocene)
Prohinnites (early Cretaceous)	
Spondylidae (middle Jurassic)	
Terquemiidae (Triassic)	
Dimyacea (late Triassic)	
Plicatulacea (Triassic)	
Ostreacea (late Triassic)	
Hippuritacea (late Jurassic)	
Chondrodontidae (early Cretaceous)	
Lithiotidae (early Jurassic)	

TABLE 4.3: Outer shell layer mineralogy and first appearance data for the cementing bivalve clades.

Most of the cementers with an aragonitic outer shell layer and so presumably aragonitic cement ,appear for the first time during the most recent phase of aragonite facilitation. The only exception is the Chamacea which first appear towards the close of the Mesozoic 'aragonite inhibiting phase'. It should be noted, however, that Section 3.5 suggests that cementation in this superfamily is not achieved by a mineralised cement. By contrast, although clearly able to exist during aragonite facilitating phases, the vast majority of those with a presumed calcite cement evolved during aragonite inhibiting phases. The exceptions to this are all members of the Pectinidae which evolved cementation during the Cainozoic. It could be suggested that the initial process of crystallization outside the confines of the extrapallial cavity is facilitated by the 'correct' seawater geochemistry.

The megalodontids, from which the rudists derive, have aragonitic outer shell layers. The rudists themselves have a thin outer calcitic layer which starts after a few millimetres shell growth. It is interesting to note that Skelton (personal communication) believes that cementation begins after the commencement of the calcite outer shell layer. Skelton (1978) regards the appearance of this outer calcitic layer in the diceratids as an "adaptive innovation.... to remain an important feature of all rudists". He suggests that this feature may have provided protection from algal boring. It is tempting to speculate that, what ever its primary adaptation, the appearance of the outer calcitic shell layer preadapted these bivalves to cement.

An interesting parallel to my observations is that of Wood (1986); she notes that calcite and aragonite calcified sponges evolve during "their respective facilitating phases". The assumption that cement and outer shell mineralogy are the same is, I believe, valid for the reasons given in 3.3.2.3; however without verification of this, this engaging link must remain unproven.

4.5.2 Geographical distribution and water temperature

Nicol (1964) notes that modern cementing bivalves are notably absent from the cold waters (<10°C) of high latitudes, but that byssally attached bivalves are not excluded

from these environments. The present study reiterates this view. By plotting the palaeolatitudes of fossil cementing genera, it is possible to show that this distribution has persisted through geological time. Figure 4.16 plots the palaeolatitude of the first recorded members of each clade, except the pseudomonotids, lithiotids and chondrodontids, reconstructing the palaeolatitudes from Smith and Briden (1977). Where the location of the first appearance is unclear it has been plotted at the highest possible latitude.

This approach is necessarily rather crude and relies heavily upon the available literature and collection biases. The results do confirm, however, that the majority of cementing bivalves originated in low latitudes, mostly between 30°N and 30°S. Notable exceptions include the oysters which are first recorded in Siberia and Arctic Canada (see Stenzel 1971), and *Chlamys pusio* which is found cementing in Icelandic waters, but in neither instance can we be sure that these are truly the first occurrences of cementation in either group. It is interesting to note that there are two independent occurrences of cementation arising in Australasia in the late Miocene. Other cementing malacofauna did occur in this region prior to this time but did not originate there. This may suggest some correlation between the innovation of the cemented habit and Australasia's progressive continental drift northwards into lower latitudes. Detailed collection is required to verify this by discovering whether the spread of the cementing stock is from the north.

Nicol accounted for the lack of cemented bivalves in polar waters as due to the inability to secrete thick shells because of the enhanced solubility of calcium carbonate in colder water or by the deleterious effect that scouring by icebergs may have on a permanently fixed bivalve.

Given the mechanism of bivalve cementation which has been established in this thesis an interesting postulate may be made for the biogeographic distribution for the first cementers. Calcium carbonate, an atypical salt, has a solubility product which decreases as water temperature increases. The mechanism of cementation described in Chapter 3 hinges upon the crystallisation of calcium carbonate from the extrapallial

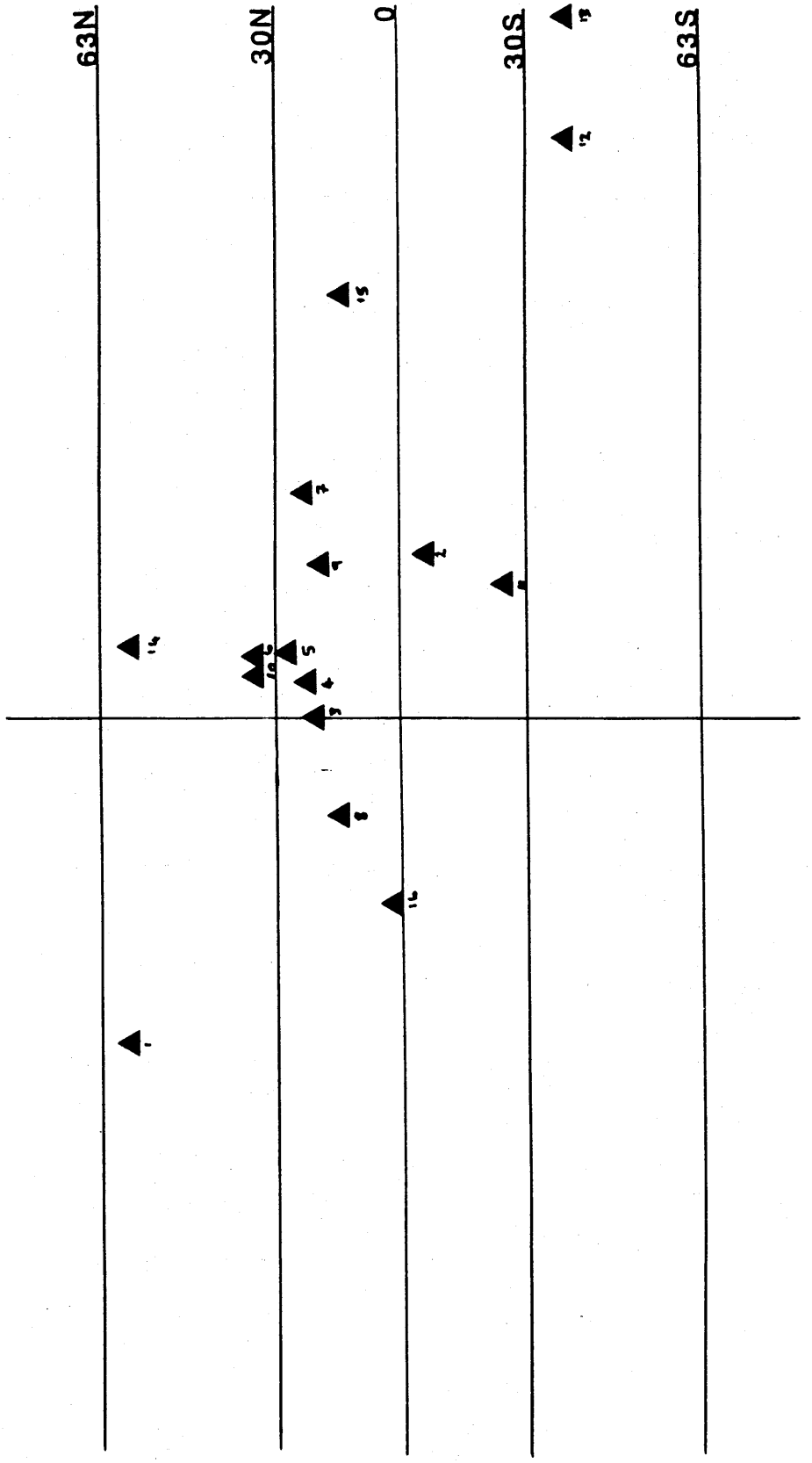


Figure 4.16: Latitudinal distribution of the origin of the each of the cemented clades, data dispersed in Chapter 2. Points plotted on the continental reconstructions of Smith and Briden (1977) and the data amalgamated. 1=Ostreacea, 2=Plicatulacea, 3=Terquemiidae, 4=Dimyidae, 5=Spondylidae, 6=*Eopecten*, 7=Hippuritacea, 8=*Prohinnites*, 9=Chamacea, 10=*Hinnites*, 11=*Etheria*, 12=Myochamidae, 13=Cleidothaeridae, 14=*Chlamys pusio* 15=*Pseudomulleria* and 16=*Acostaea*.

fluid. Higher water temperatures are likely to enhance the crystallisation of the cement thus facilitating cementation at lower latitudes. Additionally, Chapter 6 will discuss the selective advantage of cementation in the evasion of predation. According to Vermeij (1978) predation pressure today increases equatorially reaching a peak in the tropics. If predation does play a role in the evolution of the cemented habit then the origination points of each clade are more likely to be in the lower than higher latitudes.

4.6 APPLYING THIS INFORMATION TO SPECIFIC CLADES

How can this information be applied to understanding the evolution of cementation in specific clades? This chapter has identified the preadaptive requirements for cementation and established means of recognising them in the fossil record. Theoretically it should now be possible to make reasonable suggestions for the ancestral groups of certain cementing clades. Within this framework it should also be possible to make detailed studies of the evolution of the habit in these clades.

The origin of the oysters has long been problematic (see Section 2.3.3.8). A poor fossil record of the earliest forms (Carnian) has undoubtedly hampered attempts to identify the the phylogenetic origins of the clade, but so has a general ignorance of the likely features which a putative ancestor might possess. The work described in this chapter can be used to identify further avenues for thought.

Stenzel (1971) claims that all oysters attach by the left valve and that there is no evidence for the inverted form. This constancy would suggest derivation from a sinistrally pleurothetic ancestor, or at least orthothetic with some asymmetry and a bias towards the left valve. One would also predict that they would be byssally attached and, perhaps, that the earliest oysters cemented at a much later ontogenetic stage than their Recent counterparts.

Of the constructional requirements for cementation identified in this chapter it should be possible to identify likely candidates by their thin periostraca and extensible mantle margins. The former may be inferred from micro-ornament studies, whilst the latter may be indicated by the positioning of the pallial myostracum and the form of the

valve edge. Recent oysters have no pallial attachment outside the adductor myostracum. It is reasonable to suggest that the ancestral and early oysters either shared this feature or possessed a very dorsally inset pallial line.

Much of the evidence for early oysters has been gathered from high palaeolatitudes. Given the first appearance of so many of the other cemented clades in low latitudes, and the possible link that this may have with the ease of cement crystallisation, perhaps further research for putative oyster ancestors should be concentrated here.

Chapter 5 examines the family Pectinidae which has produced at least four clades of cementers. This survey will use many of the ideas developed in this chapter to examine the level of preadaptation in the family as a whole. The arguments used here can also, perhaps, be turned around to gain an understanding of the constraints which have prevented other epifaunal bivalves from acquiring the cemented habit. This is dealt with in Chapter 7.

4.7 CONCLUSIONS

1] Changes in three basic areas may trigger the onset of cementation: 'behavioural', constructional and environmental.

2] 'Behavioural':

(i) The consistency by which a clade adheres by one valve may be used to determine whether the stock is derived from pleurothetic or orthothetic ancestors.

(ii) Most, if not all, cementers derive from byssate stock and are byssally attached early in ontogeny. A contraction of this byssate phase is postulated over evolutionary time.

3] Constructional requirements and adaptations:

(i) Constructional adaptations are largely concerned with 'soft' tissue. Therefore taphonomic loss seriously inhibits the amount of information it is possible to derive from the fossil record. Nevertheless attempts have been made to retrieve such information.

(ii) A fundamental requirement of cementation is that the periostracum should be thin and permeable. Periostracal thickness *may* be determinable by studies of micro-ornament.

(iii) Further requirements concern the mantle. Extensibility may be charted by the positioning of the pallial attachment, whilst mantle 'limpness' may be assessed by the degree of valve distortion and xenomorphism. It is also postulated that information about mantle edge thickness, in particular development of the middle fold, may be gained from a study of xenomorphism. Inferences may be made about the secretion of the periostracum juxtaposing the substratum from the valve edge profiles.

4] Environmental changes

Environmental changes may facilitate the onset of cementation in preadapted clades. Relationships between the evolution of cementation and changes in seawater chemistry and water temperature are postulated in the light of the mechanism established in Chapter 3.

CHAPTER 5

MULTIPLE ACQUISITION OF THE CEMENTED HABIT IN THE PECTINIDAE

"Hinnites is probably a polyphyletic taxon containing a hodge podge of species."

Kensley (1985)

5.1 INTRODUCTION

Even within the family Pectinidae the evolution of cementation has been polyphyletic. The implication is that members of the family are supremely preadapted for the habit and have evolved cementation with relative ease.

There are two principle aims to this chapter; firstly to explore the individual clades of cementing pectinids and comment upon their evolution, and secondly to examine the family, in the light of Chapter 4, to identify the features which have allowed this iterative evolution of cementation.

5.2 EXAMINATION OF INDIVIDUAL CLADES

Section 2.3.3.2 lists four 'groups' of cementing pectinids, which I recognise as clades, which have independently evolved the cemented habit. Figure 5.1 reintroduces these clades and illustrates their stratigraphic occurrences.

Since all members of the Pectinidae are dextrally pleurothetic, monomyarian, straight hinged with prominent auricles, have ribbed ornament and are primitively byssate it is not unduly surprising that all cementing pectinids display a certain amount of convergence in form. There are only a limited number of possibilities for the morphology of a scallop cemented to the sea floor. All have an early byssate stage, resembling *Chlamys*, of varying length, which is followed by cementation by the right

valve which becomes grossly distorted. Such convergence tends to obscure their true phylogenetic relationships.

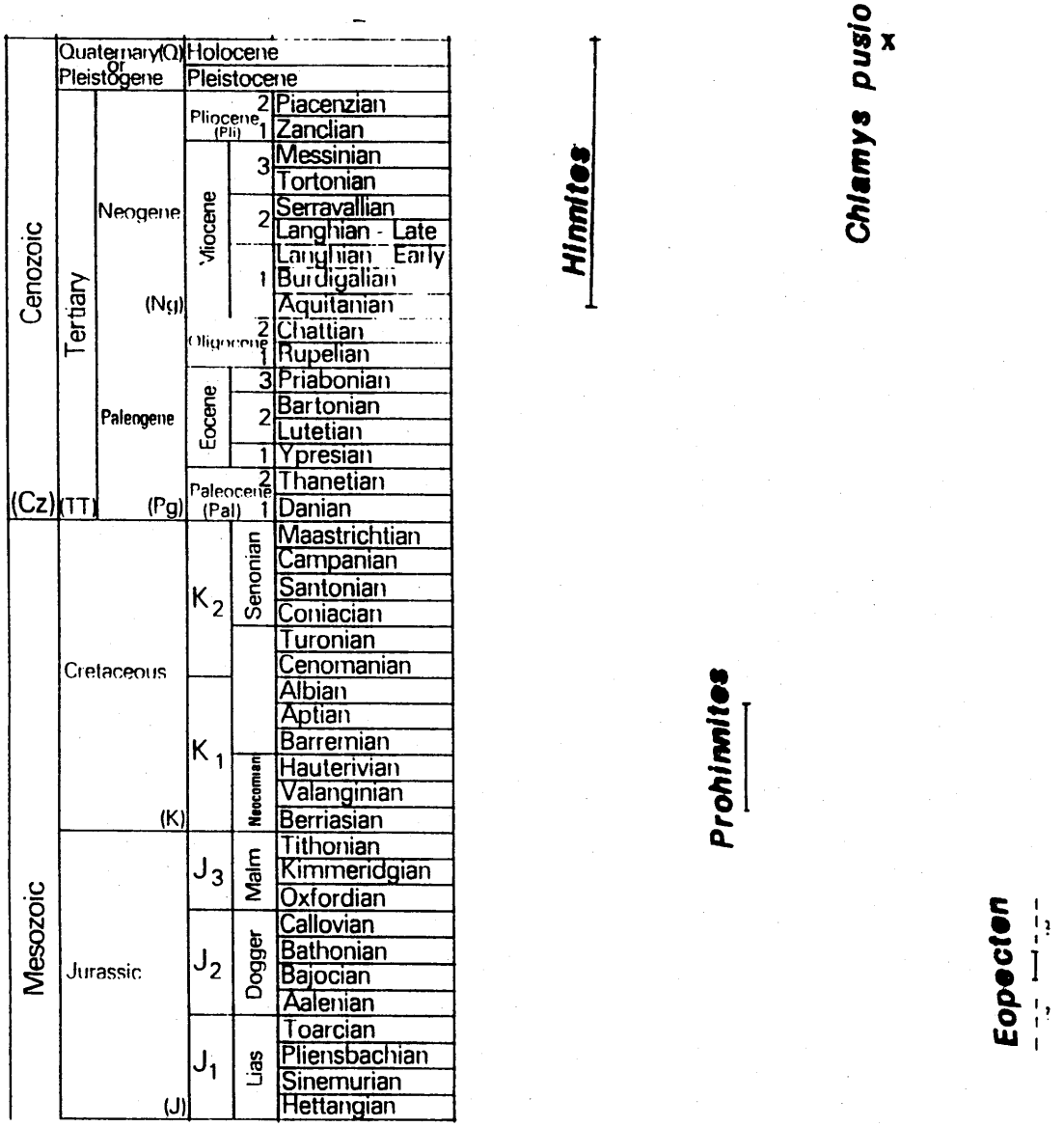


Figure 1: Clades of cementing pectinids with their stratigraphic occurrences. Data dispersed through this chapter.

Hertlein, in the *Treatise* (Moore, 1969), concludes that the Pectinidae are subject to such an extent of iterative evolution that the division of the family, pending further investigation, should be into supraspecific groups and that the possibility of polyphyly in these units should be stressed. He enumerated eleven named groups and a further

other claimed hinnitids. It is perhaps from this assemblage that future studies should select a neotype.

Figure 5.2: *Hinnites* collected from the Pliocene of Piedmont Italy. NHP specimen 34893. Valve height=110mm.

Description:

This description is based on the specimens of *H. crispus* listed above. The adult bivalve has a large thick shell. Maximum valve height of 117mm, recorded in L7522 . Height exceeds width. Dextrally pleurothetic and inequivalve, the right valve being slightly higher and more convex. Straight hinge line with prominent auricles; no byssal notch. This 'lower' valve is grossly distorted, presumably by attachment to the substrate, but there is little adherent material still present. Attachment commenced at a late stage and continued for a variable extent of the valve. Where there is no attachment scar the valve displays strong sinuous, round crested ribbing and commarginal flanges. The left valve bears a comparable ornament and occasionally exhibits a crude xenomorphism, e.g. L52221. Large triangular cardinal area, a consequence of a much migrated hinge line. Deep amphidetic ligament. The interior of both valves show a single large centrally placed adductor scar, with a large catch region discernible. The deeply incised pallial line is dorsally inset (IR =0.42, for

'uncertain' group. Those pectinids which exploit the cemented habit he placed in the *Hinnites* group, which he acknowledged to be polyphyletic.

The first described genus of cementing pectinid was *Hinnites* Defrance, 1821. This generic name has unfortunately been applied, at some time or another, to all the cementing pectinids described since. Each of the cementing pectinid clades, recognised in Figure 5.1, are described in the following sections. It must be stressed that these sections are intended not so much as taxonomic resumés but as a basis for an investigation of the evolution of their attachment. Although it may seem logical to approach these clades in the order in which they occur in the fossil record it has been decided to start with *Hinnites* - the fount of all confusion.

5.2.1 *Hinnites* Defrance

It has long been recognised that *Hinnites* is a polyphyletic genus (Reeve, 1843-78; Dall, 1915; Grant and Gale, 1931). The genus was originally described by Defrance (1821) to accommodate the type species *H. crispus*, from the Pliocene of Italy. In order to make sensible comparisons between various putative *Hinnites* a search was made for Defrance's type materal. No other author seems to have referred to it and enquiries in Italy, France and NHP have failed to locate it. N.J. Morris (personal communication) believes that it was likely to have been deposited, with the rest of Defrance's types, in the University of Caen and therefore would have been destroyed in the near obliteration of that city in 1944. I believe that at least part of the problem with the use of *Hinnites* is associated with this lack of a type.

5.2.1.1 Italian Pliocene *Hinnites*

The small collection of *Hinnites* held at the NHP contains the following specimens labelled *H. crispus*; 34893, LL25863, LL25877, L80946, L7522 and L52221. These specimens were collected, a considerable time ago, from the Pliocene of Asti, Piedmont, Italy; the type locality. This material is therefore considered adequate to gain a good impression of the genus as described by Defrance, sufficient to judge

L52221), passing around the ventral edge of the adductor. The boundary between the outer calcitic and aragonitic shell layers lies dorsal to the pallial line. Certain specimens, e.g. L80946, have radial striations on the interior face of the valve fanning out from the centre of the valves which I interpret as the impressions of radial musculature within the mantle, as described by Jaworski (1928) for fossil chamids and oysters.

The juvenile portion of the valve is regular, equivalve and undistorted by attachment. Termination of the juvenile phase is determined at the valve height where distortion first occurs (Hd). Hd was determined for the following specimens; LL25863-18mm, LL25877-17mm, L80946-19mm and L52221-26mm; a mean of 20mm. Inequilateral, having a long anterior ear separated from the disc by a deep byssal notch (later occluded by calcitic foliae). No ctenolium visible. Rounded ribs, >20 major ribs. Strong commarginal growth rings. Under inspection with the binocular microscope, specimen LL25877 displays shagreen or 'thimble' micro-ornament in the sulci between the ribs, (shagreen micro-ornament, believed to be of taxonomic importance, is illustrated in Figure 4.4(a) for *Chlamys pusio*).

From this impression of Defrance's genus *Hinnites*, it is my view that the following may also be referred to that genus rather than to another clade of cementing pectinid.

5.2.1.2 Other fossil *Hinnites*

(i) Crag *Hinnites*

A hinnitid, assigned to *Hinnites corteysii* Defrance, is described from the Crag sands of East Anglia (Pliocene) by Searles Wood (1851-1861) in his monograph of Crag Mollusca. Specimens from both the Coralline and Red Crags have been examined in both NHP LL2293, L82589,70467, 38033, L5871 and Ipswich Museum (IM): 1870-76N-18(2), 187-76-21(a), 1870-76N-20(a), 1870-76N-19, 1870-26-26, 912-31-19, 912-31-21(a). I perceive no morphological differences between the hardparts of this material and that of contemporary age collected from Italy. There are, in fact, no differences which would suggest even that they were part of another species. Well preserved specimens, such as NHP L5871, even exhibit shagreen micro-ornament in

the sulci of the juvenile shell. Hd measurements were obtained; LL2293-17mm, 38033-18mm, 1870-76N-18(2)-19mm; mean value of 18mm. Again there is evidence that attachment is tenuous, with little sign of adherent substrate. The Crags are mainly high energy sand deposits containing largely disarticulated and fragmentary shell fragments. Therefore, perhaps, one would only expect to find specimens which had less attachment and would have been more susceptible to detachment and reworking, and perhaps a preponderance of left valves. However, from the limited material available, it would seem that left and right valves are in equal abundance.

(ii) Australasian *Hinnites*

Beu and Maxwell (1990) describe *Hinnites trailli* (Hutton) from the Miocene (Altonian) of New Zealand as a distinct cementing pectinid, separate from Defrance's or the Pacific *Hinnites*, claiming a monophyletic clade which also contains the South Australian *H. corioensis*. A single specimen of the left valve of *H. trailli*, collected from the type locality (Target Gully, Omaru, NZ) is deposited in the NHP as specimen L29399. This specimen is indistinguishable from the holotype illustrated by Beu and Maxwell in Plate 17, figures a and b. The specimen is also closely similar to the Italian *Hinnites*, with an Hd measurement of 24mm and an identical ornament. The only major difference is the pronounced posterior bulge, present in both the holotype and L29399. Beu and Maxwell regard the presence of shagreen micro-ornament on the juvenile portion of the valve to be a distinctive feature. However, my subsequent studies have shown that all other Pliocene hinnitids display this feature (see above).

(iii) *South African Hinnites*

Kensley (1985) describes Pleistocene *Hinnites* from raised beach deposits in South Africa. Although he acknowledges possible polyphyly in the genus and only tentatively assigns his specimens as *Hinnites*, his figures are adequate for me to support this.

5.2.1.3 Living *Hinnites*

Von Cosel and Gofas (1984) list seven species of living *Hinnites*. Of these *'H. distortus'* can assuredly be discounted as an entirely separate clade and assigned to

Chlamys pusio, discussed in 5.2.3. Similarly Rehder's (1980) figure of '*H. pasca*', apparently endemic to Easter Island, can be excluded from the genus *Hinnites* and also bears a close similarity to *C. pusio.* Bernard (1986) also regards '*H. absconditus*' as a subspecies of *C. pusio* and reveals that *H.adamsi* is known from but a single specimen from the Antilles which is presumed derived. The remaining three can be accepted as true members of the genus *Hinnites.*

(i) Commercial rock scallop *Hinnites giganteus* Gray (see Figure 3.1)

The purple hinged rock scallop has a Recent distribution from Baja California north along the west coast of North America to Alaska. This scallop is now commercially exploited for food; hence the recent glut of fisheries literature on its biology, e.g Yonge (1951), Phleger and Rossi (1982) and Phleger and Cary (1983).

Gray (1826) seized upon the fossil genus *Hinnites* of Defrance and placed his own *Lima(?) gigantea* within it. Roth and Coan (1978) review the complex nomenclatural debate which led to the acceptance of a single species name, *H. giganteus*, for the rock scallop. The late Bernard (1986), however, chose to redescribe this bivalve as the new genus *Crassadoma,* renaming it *Crassadoma gigantea.* Yet Bernard gives no morphological differences between these specimens and the Pliocene *Hinnites;* in fact he does not record ever having studied any of the palaeontological material. Bernard's decision that the commercial rock scallop is of totally distinct origin, having been derived on the west coast of America during the Miocene, is based solely on the geographic separation between the Miocene *Hinnites* of Italy and the distribution of the modern rock scallop. Although a rather unsatisfactory argument, the genus name *Crassadoma* has gained common parlance in the aquaculture industry (N. Bourne, personal communication) and is used by Waller (1990).

My own studies of the modern rock scallop have utilised Gray's holotype (NHZ 1950-2.1.1), along with a number of conspecifics also held in the NHZ collections (most unregistered, but including lots 2258 and 2238). Additionally I was also able to obtain a suite of growth stages from the Canadian Department of Fisheries. These comprise a number of uninhabited valves at 6-8 months (HIN10), 1-1.5 years

(HIN11) and fully mature (HIN12) and a number of wet samples (HIN13 and HIN14). Although Bernard asserts that his genus originates in the Miocene of California I have been unable to locate any palaeontological material. However, Grant and Gale (1931) do illustrate Pleistocene material they identify as *Hinnites multirugosus*, undoubtedly the same species.

Having been able to assemble specimens of Bernard's *Crassadoma,* including the type, and the Italian Pliocene *Hinnites* in one place for direct comparison, my conclusions are that the morphology of *'Crassadoma gigantea'* is identical to that of the Italian Pliocene *Hinnites* described in Section 5.2.1 and that Bernard's erection of a new genus to accommodate the former was unjustified.

(ii) *H. corallinus*

I have been unable to locate actual specimens of this species which is found in the Indian Ocean and Japan, but the illustration in Reeve (1853), Plate 1, strongly suggests that it is a true hinnitid. The species has been recently recorded in Japanese waters for the first time after an absence of many years (Okutani and Osato, 1988).

(iii) *H. spectabilis*

Von Cosel and Gofas (1984) describe a new species *H. spectabilis* from the waters off Angola. I have inspected the holotype and four paratypes from MNHN (unnumbered) and confirm their membership of the genus.

5.2.1.4 *Summary of* Hinnites

Figure 5.3 depicts the geographical distribution of those bivalves recognised in the preceding sections as belonging to the genus *Hinnites*. Their distribution is far more widespread than was previously recognised. This undermines Bernard's contention (1986) that the rock scallop must be of entirely different origins to that of the Italian *Hinnites* because of their seemingly isolated occurrences. Perusal of land-sea maps reconstructed for the Miocene/Pliocene (e.g. Smith and Briden, 1977) clearly shows a connecting sea way between North and South America which connected Atlantic and Pacific. Studies of both modern and Pleistocene Arctic faunas, e.g. Lubinsky (1980)

and Wagner (1970), do not record the genus in the seaways to the north of Canada. It is perhaps a general lack of exposed Late Tertiary rock which produces an artifically patchy distribution.

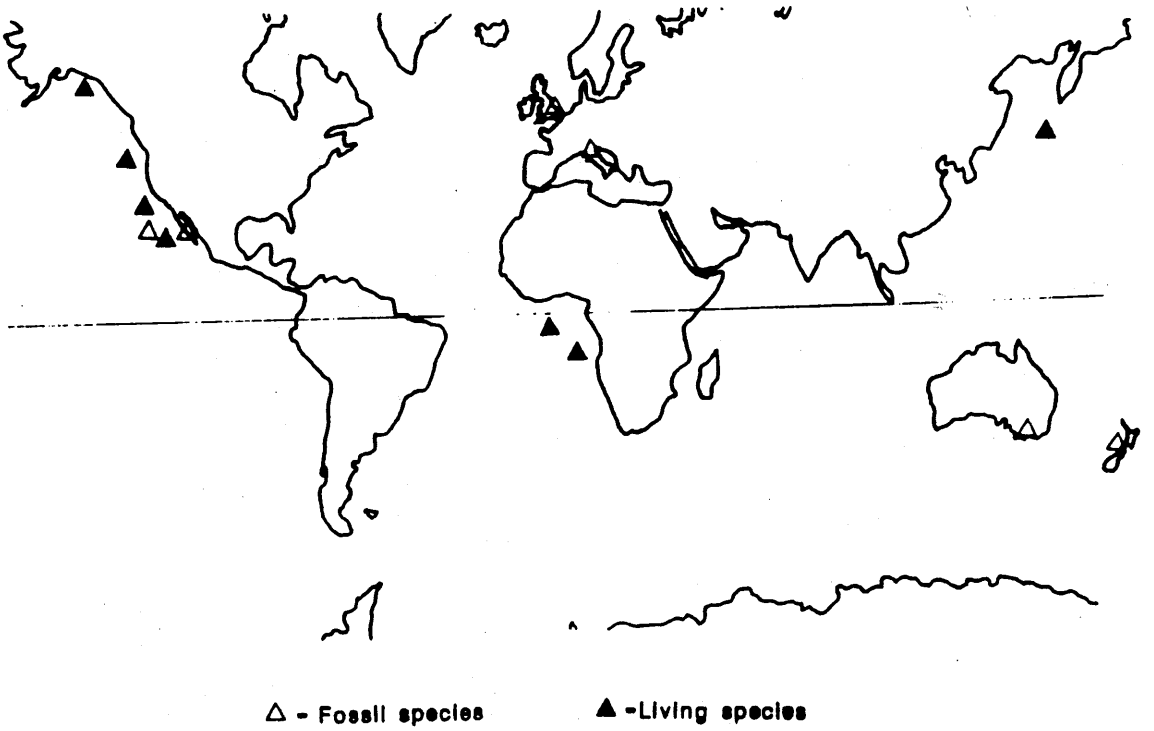
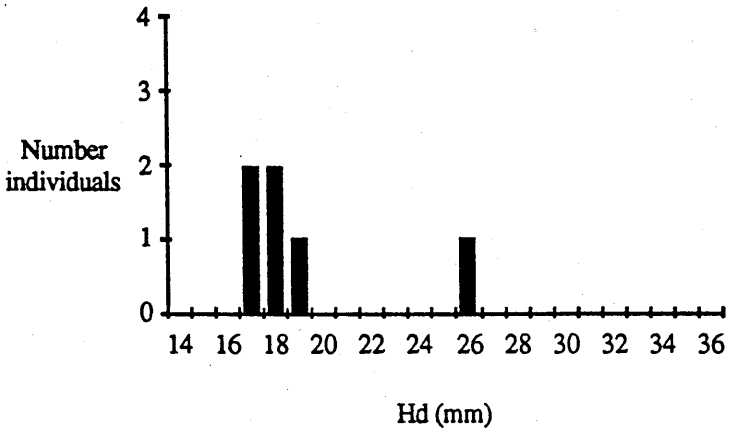


Figure 5.3: Geographical distribution of both living and fossil cementing pectinids recognised as true *Hinnites*.

All of the observed *Hinnites* have early byssate phases. Figure 5.4 show two histograms plotting the attachment height (Hd) of a) fossil and b) Recent hinnitids. Although the data set for the former is small, there may not be any significant difference in stage of attachment between the two groups.

A)



B)

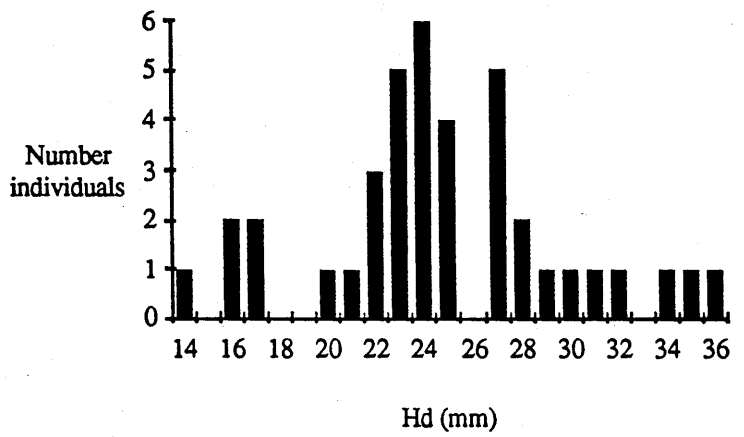


Figure 5.4: Histogram plots of valve height of attachment (Hd) in A) Pliocene and Pleistocene hinnitids (N=6) and B) Recent hinnitids (N=40). Data derived from specimens mentioned in the text.

Yonge (1951) suggests that the stimulus for cementation may be the onset of sexual maturity. I have no data either to support or refute this, but it would seem that environmental conditions are a major control of the process. Availability of a suitable substrate apparently overrides any genetically predetermined command. Specimens in sample HIN011 reach valve heights of 35,32,32,38,41and 31mm with no sign of distortion. These individuals were obtained from commercial ear-hanging cultures, i.e. had no opportunity to cement. If the onset of cementation is triggered by a definite genetic command then one would expect at least some of these individuals to lose their regular valve form.

Occlusion of the byssal notch on cementation is achieved by growth of irregular, rugose shell material. Samples removed from the occluded notch of *Hinnites giganteus* were analysed to determine whether the occluding matter is aragonite or calcite. Negative staining with Feigl's solution and XRD analysis, (run on my behalf by A. Abrahams, Cambridge University), has demonstrated that this infill is calcitic. The only perceived major differences in the attachment between the fossil and living members of the genus is perhaps an increase in strength and extent of cementation. All fossil material examined is largely clear of adherent substrate whereas the living rock scallop requires "a hammer and chisel to dislodge" (N. Bourne, personal communication). Whether this change is genuine or due to a taphonomic bias or a artefact of museum preparation is unknown at present.

Evolution of the genus: As with other cementing bivalves I believe that it is the pre-cementation valve form of *Hinnites* which can be most useful in determining the close phylogenetic relationships, whose characters are generally masked by gross distortion and xenomorphism. The 'juvenile' byssate phase of *Hinnites* is conspicuously *Chlamys*-like. Dhondt (1973) in her revision of the latter genus refers to it as comprising members of the Pectinidae with strong radial ribs, unequal auricles, deep anterior byssal notch in the right valve and valve height that exceeds width. She follows Glibert and Van der Poel (1965) in acceptance of shagreen micro-ornament as characteristic of the genus. The 'juveniles' of *Hinnites* (both fossil and modern) display all these features, and it seems reasonable to suggest a *Chlamys* ancestry for the genus. Indeed Waller (1990) has already postulated an origin for *H. giganteus* from the contemporaneous *C. hastata*. Yonge (1951), however, favours a *Pecten* origin for the species. Perhaps our best chance of identifying the closest non-cementing relation would be to examine actual juvenile specimens of Tertiary forms. However, all material in collections recognised as hinnitid is mature, hardly surprisingly as only those specimens which have attained cementation are likely to identified as such. It is to be presumed that pre-cementation *Hinnites* do exist and that they have been curated into different genera. Nevertheless, deliberate searches in

NHP amongst other pectinid material from relevant ages and deposits has, as yet, failed to reveal likely candidates.

Summary of section information:

Hinnites is a cosmopolitan genus probably arising from *Chlamys* stock in the Miocene/Pliocene. Although it is fully recognised that the generic name has become polyphyletic to the extent that it has been applied to all cementing pectinids, all of the above are considered true hinnitids. In the past, over-enthusiasm for the polyphyletic nature of cementation in pectinids has led to claims that each of the above are separate evolutionary lineages.

5.2.2 *Prohinnites* Gillet

Hertlein in Moore (1969) recognises the Lower Cretaceous cementing pectinid genus *Prohinnites* (Valanginian-Aptian) as distinct from the Tertiary *Hinnites*. Only a limited amout of material of the former genus has been available for my inspection (NHP specimens; L6888, L51834, L5147, L5180 L5872, L438, L6271, L53883 and L3449), collected from Oman, Tanzania and the Isle of Wight. Consequently very little can be said about this apparent clade. The valves are large, 100-170mm in height, and grossly inequivalve. The right valve is very convex, with an abrupt raising of the ventral valve margins following the cessation of cementation. Details of the stage and extent of attachment are obscured. Only two specimens, L438 and L5180, show any sign of a juvenile uncemented phase. In the latter it would appear that cementation followed a byssate stage, similar to that observed in *Hinnites*. This observation is in direct contrast to that of Cox (in Moore, 1969 (N102)), who states specifically that *Prohinnites* lacked a byssal notch.The exterior of the right valve bears coarse round crested ribs, about 8mm across. The left valve is virtually flat, and slightly shorter than the right. No expression of the early uncemented phases are reflected. The external ornament is identical to that of the right, but for the possession of many hollow, tubular spines arising from the ribs (see specimen L5872 and L438). Both valves are thick, despite in most cases having their internal shell layers absent. The right valve of L53183 is at least 25mm thick. The hinge line displays a large area,

with a deep centrally placed ligament pit. The inner aragonite(?) shell layers extend close to the ventral valve margins. In one specimen, L51847, a large centrally placed muscle scar is visible, but there are no details of a pallial line.

5.2.3 *Chlamys pusio* (Linné)

Although most modern authors (e.g. Tebble, 1966) refer to this species as *Chlamys distorta* Da Costa it appears in the 1758 10th Edition of Linné's *Systema Naturae* (p.698) as *Ostrea pusio*. According to my understanding of taxonomic precedent the specific name *pusio* should be adopted.

5.2.3.1 Recent examples

The life habits and soft part morphology of Recent individuals of *Chlamys pusio* have been observed from living specimens in Galway Bay (subsequently collected as lot CD015) and pickled from Port Erin (Isle of Man) lot CD016. This material was supplemented for valve study with the immense number of NHZ specimens, largely from the T.G.W. Fowler collection, (this collection is localised but unnumbered).

Valve morphology see Figure 5.5

Inequilateral, more or less inequivalve and thin shelled. Typically chlamyid in appearance; having a long straight hinge line, asymmetric auricles; the anterior auricle of the right valve being elongate and separated from the disc by a deep ctenoliate byssal notch. Height exceeds width. Umbonal angle 90°. Shagreen micro-ornament, see figure 4.4(a). The right valve varies considerably from being virtually flat to very convex and is commonly highly distorted. Sinuous fine ribbing; alternating small and coarse, with sharp angular crests, see Figure 5.6. Rib count on mature specimens numbers approximetly 60. Short thorn-like spines may arise on the ribs, particularly on more mature parts of the valve. The left valve is usually flat, occasionally displaying a crude xenomorphism. Its ornament is identical to that of the right, except for a lack of spines. Brightly coloured.

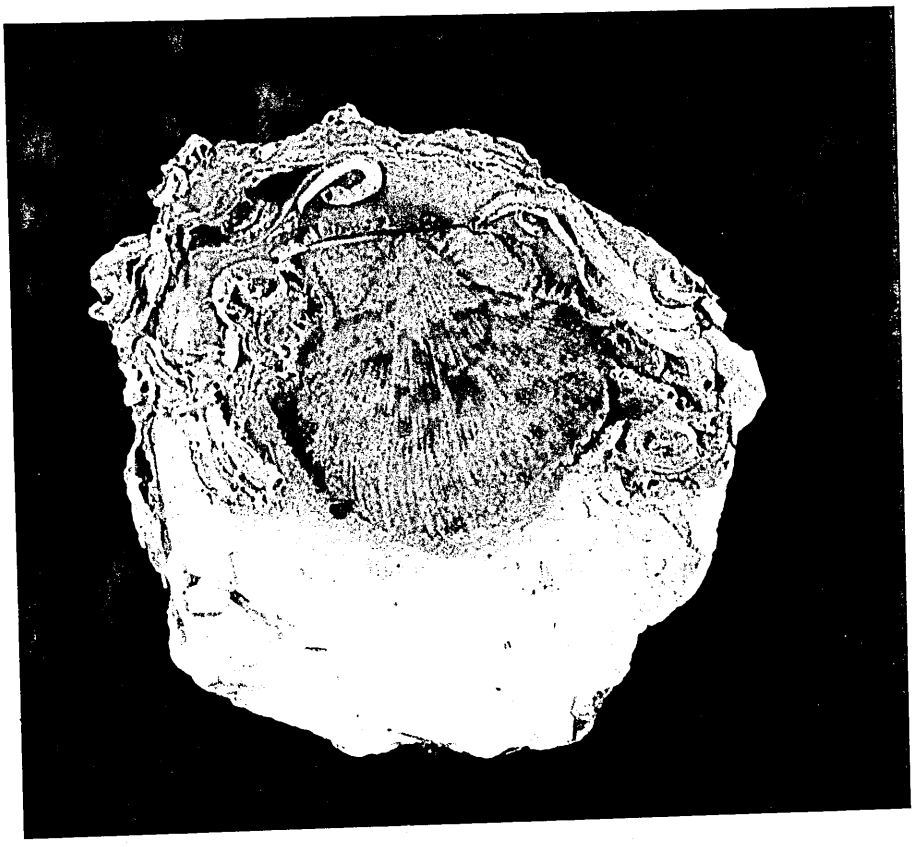


Figure 5.5: *Chlamys pusio* attached to the inside of a serpulid encrusted *Ostrea edulis*, unregistered specimen from NHP. Valve height=30mm

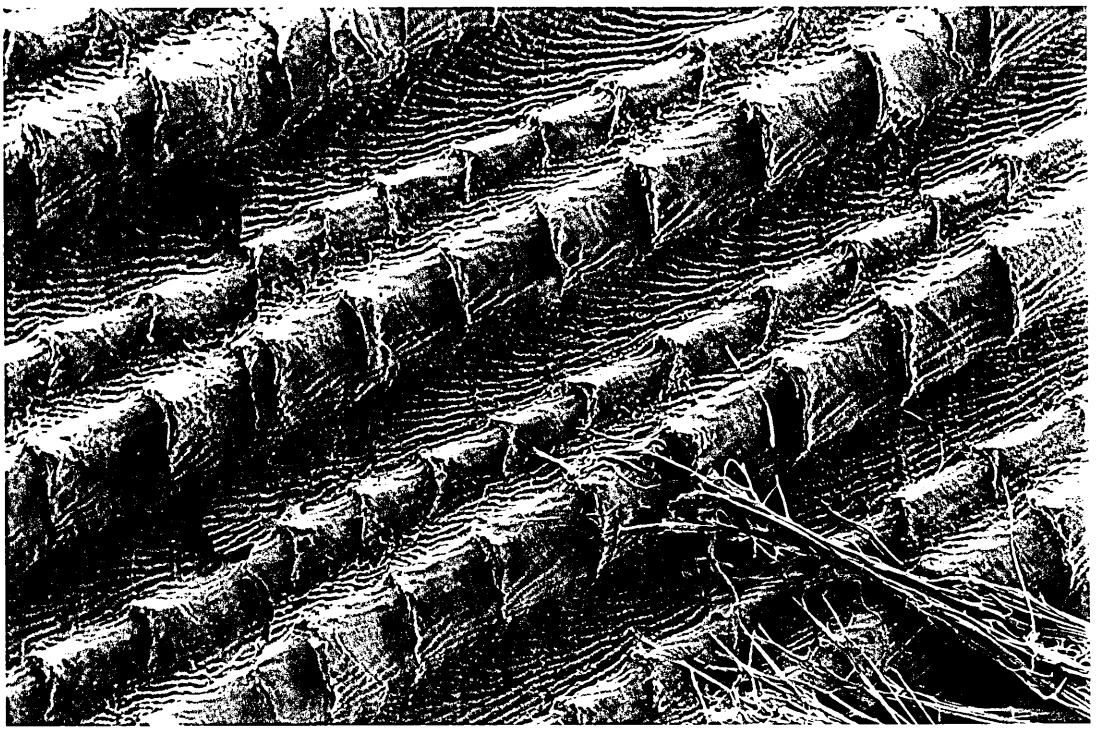


Figure 5.6 Ornament of *Chlamys pusio*. Stub EMH0212. 25mm=500µm

Soft part anatomy

Vivisection and SEM studies (e.g. stubs EMH0030, 0055, 0056 and 0058) show that the species has an active mantle margin, the middle lobe of which bears tentacles and ocelli. The foot is small but active.

Geographical range

Tebble (1966) quotes the species as ranging from southern Icelandic waters in the north to the Mediterranean and Azores in the south.

Life habits and changing morphology

Chlamys pusio is dextrally pleurothetic throughout life. The early stages, up to an average of 16mm valve height, are virtually equivalve and undistorted. Attachment is via a byssus emerging from the byssal notch and splayed by the ctenolium. Individuals at this stage of development were observed in Galway Bay to be firmly fixed in crevices and excavations in the substrate. At a valve height averaging 16mm for the 286 specimens measured, ranging from 10 to 27mm (data displayed in Figure 5.10) the right valve commences distortion which continues over a variable valve height. This distortion coincides with the onset of xenomorphism in the left valve, the emergence of spines on the right valve and the occlusion of the byssal notch (Figure 5.7). The rugose fasciole material which occludes the byssal notch does not stain with Feigl's solution and therefore is presumed to be calcitic, like that of *Hinnites giganteus*.

Field observations imply that, contrary to the views of other authors, e.g.Tebble(1966), the mature specimens of *Chlamys pusio* are not invariably cemented. Rather the cemented habit is facultative; some individuals being firmly cemented (see Figure 5.5), others lying free, lodged by their distortion into crevices. I am confident that the latter group are not merely detached specimens of the former as they bear no scar or adherent substrata.

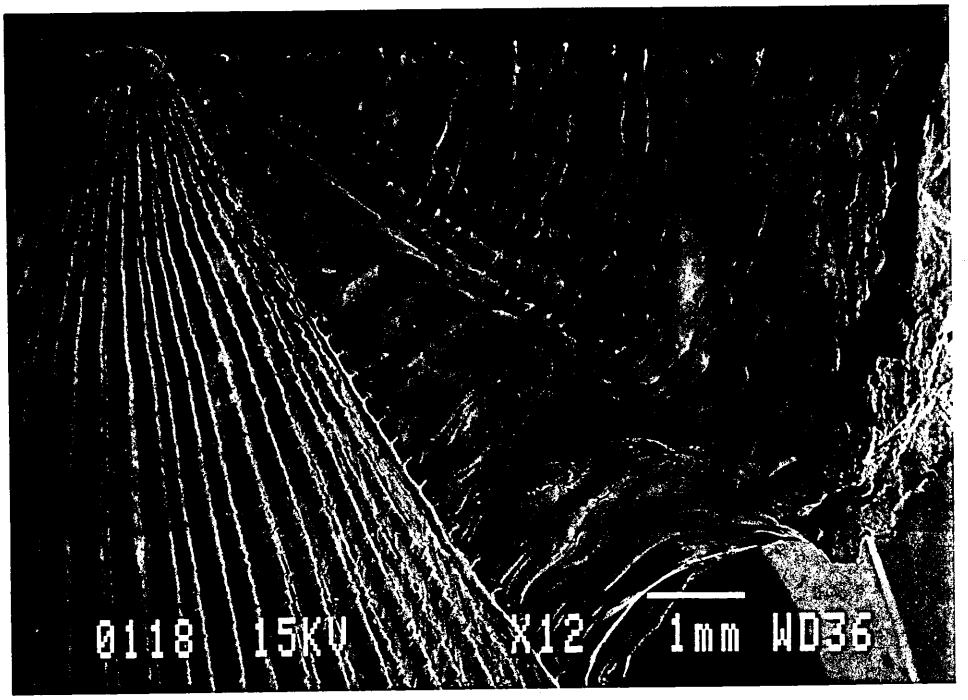


Figure 5.7: Occlusion of the byssal notch and ctenolium in a cementing individual of *Chlamys pusio*. Stub EMH0118.

Figure 5.8: Scanning electron micrograph of the underside of *C.pusio* removed from its substrate. Stub EMH0413. Note total loss of idiomorphic ornament during cementation and the perfect moulding around barnacle (B) and serpulids (S).

Bernard (1986) maintains that cementation in this species is effected by the idiomorphic growth interlocking with substratal irregularities, i.e. Model 5 of Section 3.2.2. My own observations show that this is not the case; perhaps Bernard may have been referring to the free lying specimens, mistakenly believing them to be cemented. Figure 5.8 illustrates the base of the right valve of a cemented specimen (Stub

EMH0412). The specimen has been prepared by prising it from its substrate (the interior of an oyster), followed by immersion in KOH to remove all organic material. The figure demonstrates that the radial ribbed ornament is absent during attachment and that the valve has taken up the smooth surface of the substrate, moulding around barnacles and a filamentous obstruction also fouling the oyster shell.

5.2.3.2 Palaeontological material

Da Costa (1778, p.150) states "This kind [*Chlamys pusio*] is pretty frequently found in the chalk pits of Kent and Sussex'. However, searches of Chalk bivalves have failed to reveal any specimens which might conceivably belong to this species. Searles Wood (1851-61) refers to *Pecten pusio*, a synonym of *Chlamys pusio*, from both the Coralline and Red Crags. The specimen he figures is neither cemented nor distorted, but in all other respects is akin to the modern examples.

Palaeontological material has been examined by me from the collections of NHP, SD, IM, BCM and my own personal childhood collection. Apart from any specimens which may be held in the Norwich Castle Museum this probably represents the vast bulk of material held in this country. Virtually all these specimens were collected from the Pliocene/Pleistocene Crag of Suffolk, but SD specimens C52535-52540 derive from Belgium, whilst NHP houses a small number of unnumbered individuals from Italy.

a) b)

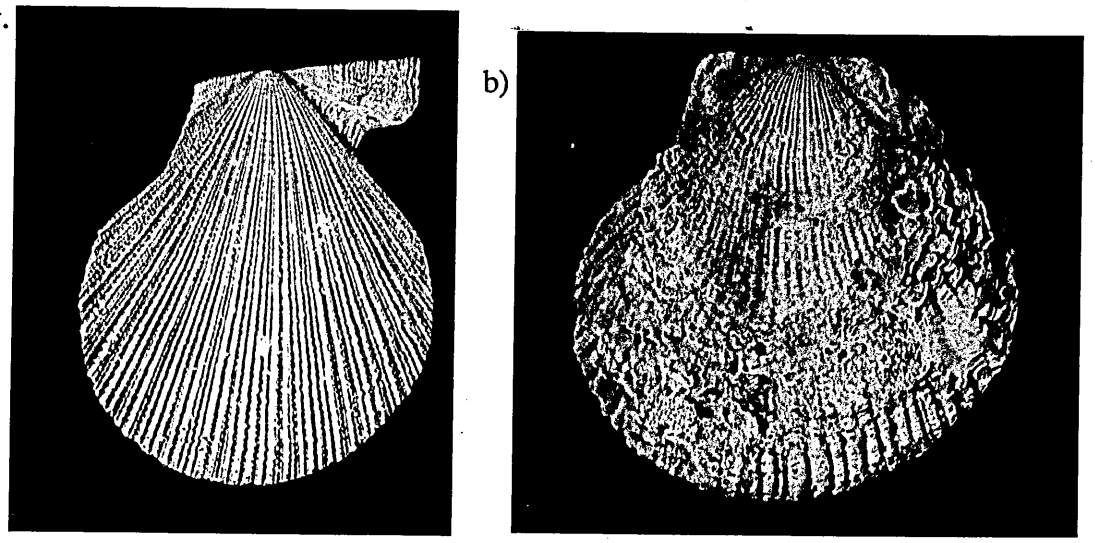


Figure 5.9: Fossil and Recent *Chlamys pusio*. a] EMH017 collected from the Coralline Crag at Sudbourne Park (TM405514), when I was nine. Valve height =31mm. b] EMH016 collected from Galway Bay. Valve height=32.5mm.

Figure 5.9 illustrates the right valve of both fossil and Recent cementing examples of the species and clearly shows the fundamental differences between the two. Yet comparison of Figure 5.9(a) with the Recent specimens prior to cementation shows the similarity of ornament (see Figure 5.6) and undistorted shell form. My observations tally with those of Searles Wood. The fossil *Chlamys pusio* appear to be have been byssally attached throughout ontogeny, maintaining an equivalve and undistorted morphology with an open byssal notch and active ctenolium. Although certain left valve specimens, e.g. SD C36626,C36629,C44798 and C71216 do display a certain amount of distortion, which may be interpreted as xenomorphism, it is minimal and quite comparable with valve distortion seen in other pleurothetic byssally attached pectinids. In over fifty right valves examined there is no evidence of cementation.

Three hypotheses may be advanced to account for these apparent differences in habit between fossil and modern forms:

(i) The fossil specimens observed are representative only of the pre-cementation byssate phase.

(ii) The Crag seas were devoid of suitable hard substrates on which to cement and therefore the byssate ecomorph was predominant.

(iii) Pliocene/Pleistocene *Chlamys pusio* genuinely lacked the ability to cement.

Figure 5.10 is a histogram which plots the frequency distributions of Hd for 286 Recent specimens along with the valve height for 51 fossil individuals. It is evident from this that the vast majority of the fossils have attained a valve height greater than that at which modern individuals have started to cement. On the basis of this I reject hypothesis (i).

There was no shortage of hard substrates in the Crag deposits, as indicated by abundant encrusting epifauna, including the bivalves *Anomia, Ostrea* and *Hinnites,* as well as large *Balanus* and bryozoans . As stated previously (Section 5.2.1.2) the Crag sands are high energy sand wave deposits so that one might predict that if

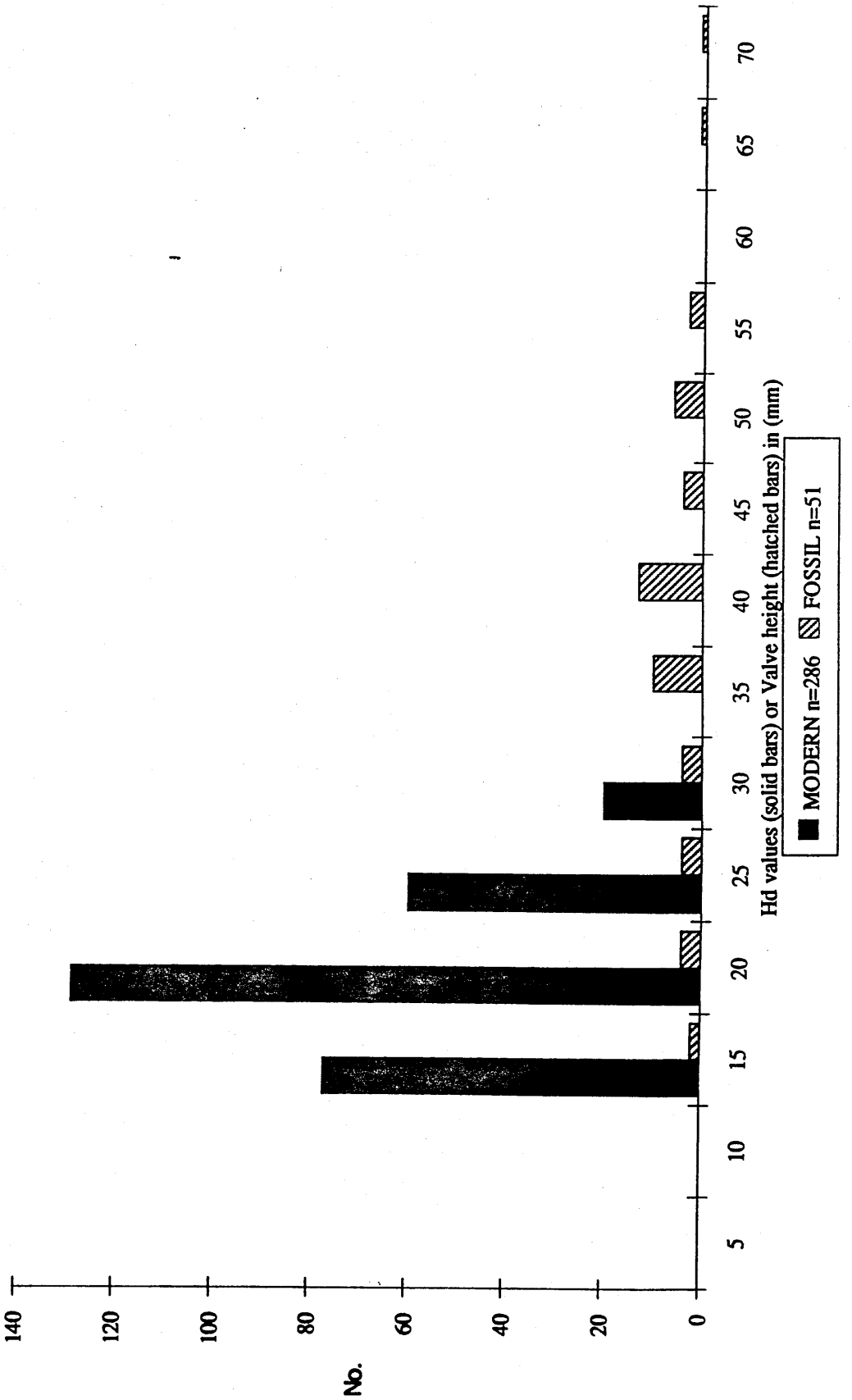


Figure 5.10: Histogram to show the valve heights of fossil *Chlamys pusio* and the attachment height (or Hd) of Recent specimens.

C.pusio had the ability to cement collections would be biased towards the more easily transported left valves. However, the largest collection of valves, 51 in the Sedgwick collection, contains 25 right valves thus implying that no such bias exists. On these grounds hypothesis (ii) is rejected.

This leaves hypothesis (iii) as favoured, implying that the ability to cement in *Chlamys pusio*, is a relatively recent, i.e. post Pliocene/Pleistocene, acquisition. The facultative cementation observed within the species may thus be a signal of the inception of a new cemented clade.

5.2.4 *'Eopecten'*

This section describes an apparently previously undescribed large cemented pectinid from the Middle Jurassic of Normandy and southern England. I am most grateful to T.J. Palmer, who first observed these bivalves, for drawing them to my attention.

5.2.4.1 Occurrence

SPECIMEN	LOCALITY	CONDITION	TYPE
BB1/90	Campagnettes	Missing umbo	A
BB2/90	Lion-sur-Mer	Ventral fragment	A
BB3/90	Campagnettes	Fragment	B
BB4/90	Luc-sur-mer	Fragment	A
BB5/90	Lion-sur-mer	Umbo region	A
BB6/90	Campagnettes	Complete-abraded	B
BB7/90	Luc-sur-mer	Umbonal fragment	A
BB8/90	Luc-sur-mer	Umbonal fragment	A
BB9/90	St.Aubin	Byssal notch region	A
BB10/90	Luc-sur-mer	Complete-bored & encrusted	A
BB11/90	Luc-sur-mer	Two attached	A
BB12/90	Campagnettes	Complete	A
BB13/89	Campagnettes	Whole-fragmented	B
BB14/89	Campagnettes	Whole-fragmented	B
BB15/90	Breakheart Hill†	Umbo missing	A

Additional material: Thin section TS25 off TJP specimen TH, acetate peels 1 & 2 and stubs EMH0330, EMH0331, EMH0408-413 (inclusive), see Appendix 1.
† collected by TJP.
Table 5.1. Collection details of material studied here. Locality details given in text.

Table 5.1 summarises the collection data for the material utilised in this study. Further details about the localities are provided below:

Normandy All but one specimen were collected from Normandy in the Upper and Middle Bathonian rocks surrounding Caen. The sedimentology and palaeoecology of these strata were studied in detail by Palmer (1974), who divides them into seven members; Revier, Fontaine Henri, Blainville, Campagnettes, Ranville, St.Aubin and Langrune (in order of decreasing age). Localities which yielded the cementing pectinids were:

(i) Lion-sur-mer to Luc-sur-mer coastal section

Specimens were collected from hardgrounds within Palmer's Langrune member exposed on the foreshore between Luc and Lion, below the low cliffs composed of a coarse, cross bedded biosparite. Whole specimens were more prevalent at the western Luc end of the section, on a hardground developed at the top of the sponge reef (i.e. at the base of the member).

(ii) St. Aubin

An abraded hardground lies at the base of the St. Aubin Sponge reef exposed in the Falaise de Catel, the St. Aubin Member of Palmer. This hardground is exposed at low tide in the foreshore.

(iii) Carrière de Campagnettes

An inland site (x=1174.5; y=411.5), west of the N814, near the village of Amfréville. This quarry exposes the Ranville, Campagnettes and Blainville members, i.e. older units than those exposed on the coast. The floor of the working is littered by dislodged blocks of hardground material, riddled with lithophagid borings, on which the large pectinid was found. Palmer (personal communication) believes these blocks to be derived from the hardground which lies on top of the Blainville Member.

UK A further specimen has been collected from a hardground within the Inferior Oolite of Breakheart Quarry, Dursley in Gloucestershire (ST755968) by TJP.

5.2.4.2 Morphology

All material described here is to be housed in the NHP as a single lot. Individuals may be recognised by their field numbers which are prefixed by BB and suffixed by the year of their collection.

Two distinct morphologies have been identified and these are described separately.

Type A - 11 specimens

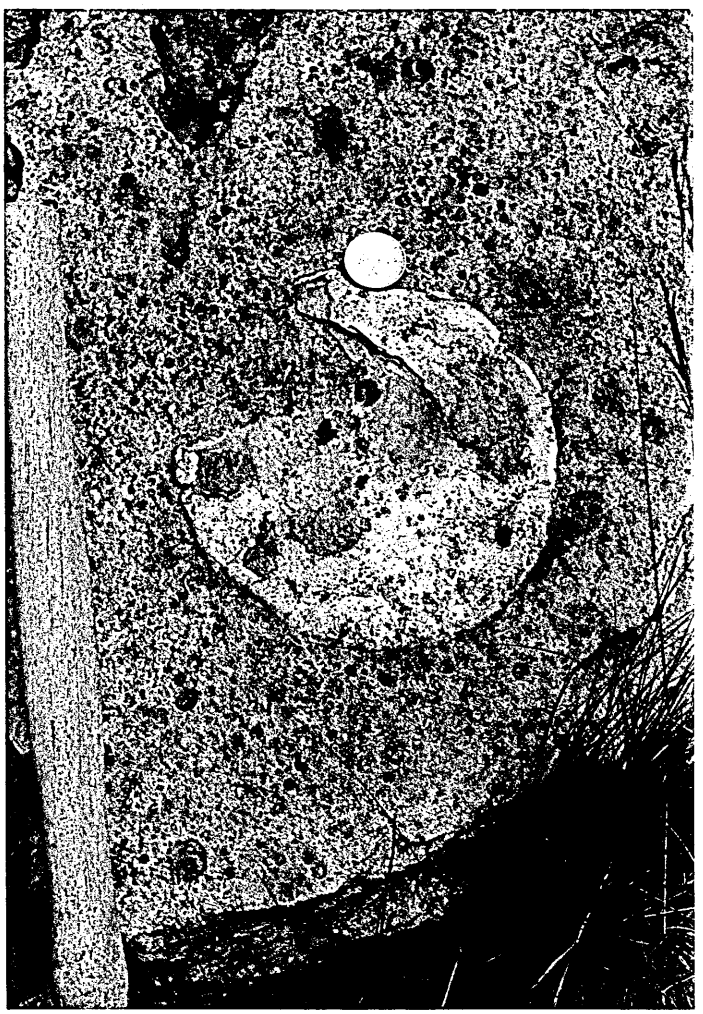


Figure 5.11: Specimen BB1/90 *'Eopecten* A'attached to a block of hardground in Carrière de Campagnettes. Valve height=180mm.

The right valves of A type specimens are large, thick and oval shaped and are found attached to hard substrata (see Figure 5.11). The valve height, which reaches a maximum of 180mm in specimen BB1/90, with a mean of 175mm, exceeds the length

by at least fifty percent. The valves are usually flattish, gently lifting ventrally to form a very shallow bowl.

Internal features

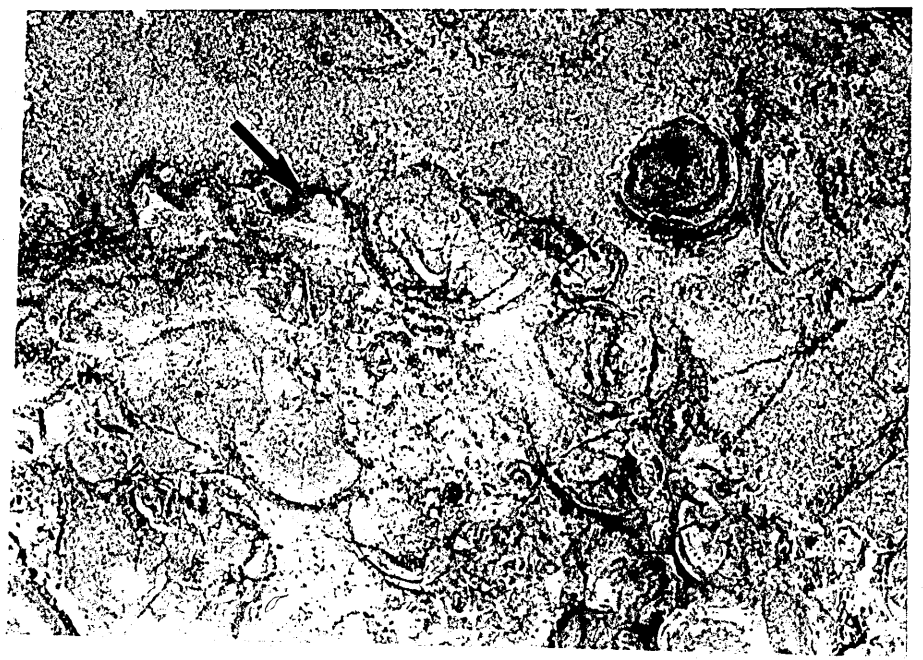


Figure 5.12: Details of the inner surface of BB8/90 '*Eopecten* A'. Encrustation of the inner surface of the outer shell layer, implying early aragonite dissolution. Arrow marks boundary between inner and outer shell layers. Width of field of view=40mm.

A large central portion of the inner shell layer in each specimen has been lost by diagenetic dissolution, leaving a raised band around the edges of the valve, widest at the ventral edge where it reaches up to 40mm. The inner face of this band which juxtaposes the missing layer(s) has a stepped profile. This residual band is composed of calcite and it is therefore assumed that the missing material was originally aragonite. Dissolution of this aragonite must have been rapid following the animal's death and must have taken place whilst still exposed on the sea floor, as evidenced by the colonization of the exposed calcite by other epibionts such as *Atreta, Lopha*, serpulids, corals and plicatulids (see Figure 5.12). This early loss of aragonite has already been described from these localities by Palmer, Hudson and Wilson (1988). Removal of the inner shell layers in this way has deprived us of any information on the dentition or

pallial and adductor myostraca, but it is clear that the former myostraca must have lain dorsally to the calcite/aragonite boundary.

Specimen BB11/90 shows radiating striations on the outer calcite band. These are interpreted as the impressions of radial muscles within the mantle .

External features

The external side of the right valve can be divided into three zones:

(i) Byssate zone

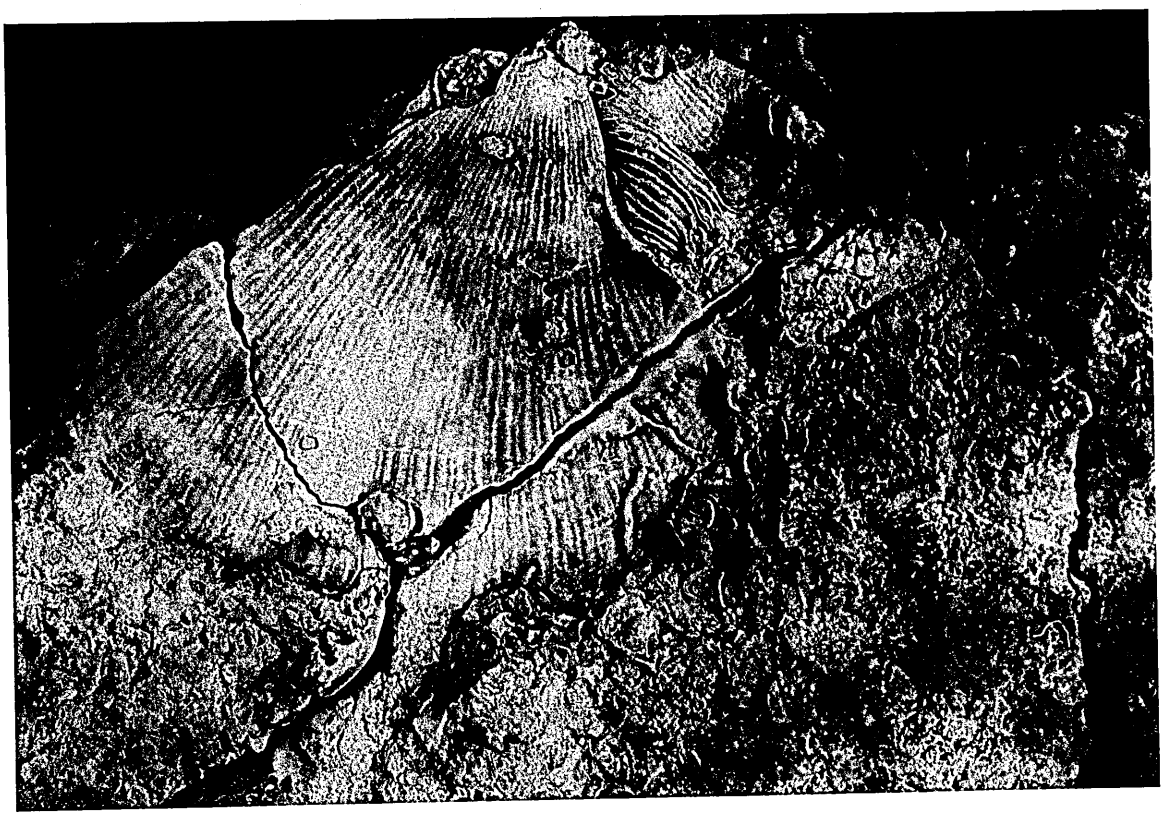


Figure 5.13: Juvenile byssate portion of the right valve. Specimen BB11/90. Height of discernible *'Chlamys'* stage = 75mm.

A thin '*Chlamys*' like early growth stage is identifiable dorsally at the umbo (Figure 5.13), although in many specimens this has been partly lost by breakage. The features of this stage are best observed in specimen BB11/90. This most juvenile stage is thin shelled (<2mm thick) and ornamented with fine ribbing. The ribs are slightly sinuous and appear beaded. Ribs appear in alternating couplets of very fine (<0.5mm) and slightly coarser 1mm) width. This form of double ribbing is reminiscent of that observed in *Chlamys pusio*. No shagreen micro-ornament observed.

The hinge line is long and straight. Auricles are clearly present, bearing a ribbed ornament. The anterior auricle is elongate and is separated from the disc by a deep byssal notch which is occluded later in life. At least seven teeth flank the notch, on the disc side, to form a ctenolium (see Figure 5.14).

Figure 5.14: Details of the byssal notch of specimen BB11/90 '*Eopecten* A'. Note the presence of a ctenolium (arrowed) and the growth of a rugose fasciole occluding the notch. Width of field of view =70mm.

This juvenile byssate stage is terminated abruptly where the cemented shell commences. The mean height of the valve at attachment is 44mm, although a certain amount of variation is recorded.

(ii) Cemented zone

Following the byssate zone there is a concentric saddle of the attached zone identified by adherent substratum. It has not been possible to remove fully all the substratum from any individual but exploratory preparation indicates that the fine ribbing observed in the earlier growth stages is absent. Study of thin section TS25 shows that the valve follows substratal topography with a high degree of accuracy. For example shell material is seen to drape into borings.

During this phase of growth the bivalve maintained a straight hinge line. The byssal notch became occluded by a rugose fasciole (see figure 5.14) whilst the anterior auricle became more irregular, until it was no longer a distinct feature.

Extent of attachment varies markedly between specimens, being most sparse in BB8/90 and most well developed in BB1/90.

(iii) Ventral 'lift off' zone

Most specimens, in particular those collected at Luc, display evidence of post-attachment growth where cementation ceased and the valve lifted clear of the substrate. Once this had occurred there is no evidence of individuals reattaching. This lift off is emphasised in specimen BB8/90, where the underside of the ventral part of the valve has become colonised by contemporaneous epibionts such as *Lopha,* serpulids and bryozoans. The valve ornament is characterised by broad commarginal flanges and coarse ribbing. These ribs are 4-8mm in width and have rounded crests.

Shell structure

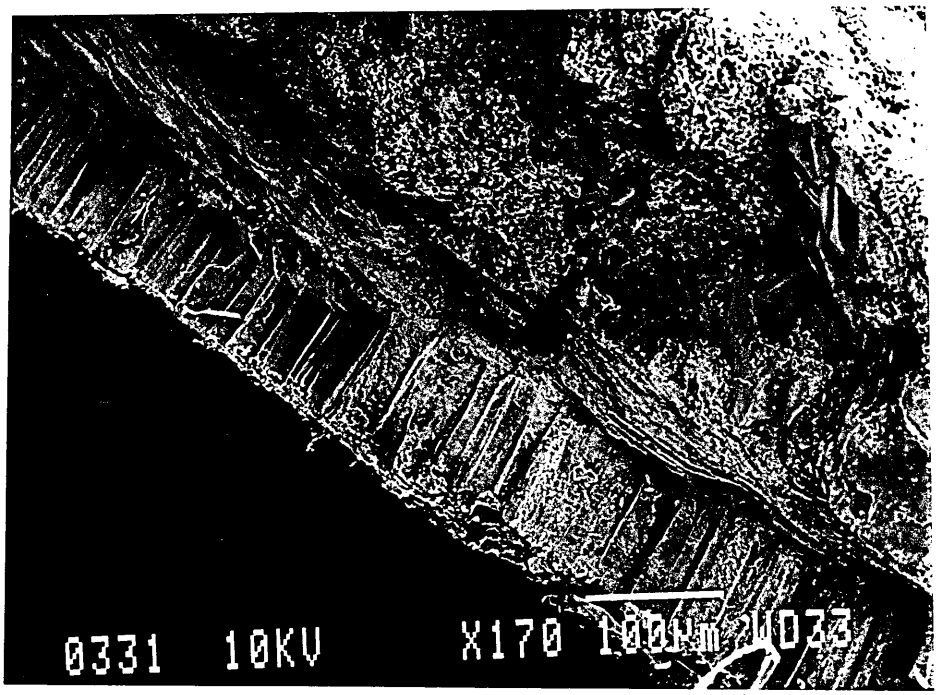


Figure 5.15: Shell structure of the pre-cementation phase in '*Eopecten* A'. Fractured preparation, Stub EMH0330.

The outer calcitic shell layer attains a great thickness, up to 15mm. Examination of TS25 and SEM stubs EMH0330 and EMH0331 reveals that the bulk of this calcite

displays foliated shell microstructure. Fractures across the 'byssate' part of the valve (e.g.EMH0330) reveals a thin outer prismatic layer, (see Figure 5.15). This prismatic shell layer is absent from part of the shell formed after the commencement of cementation.

Type B- 4 specimens

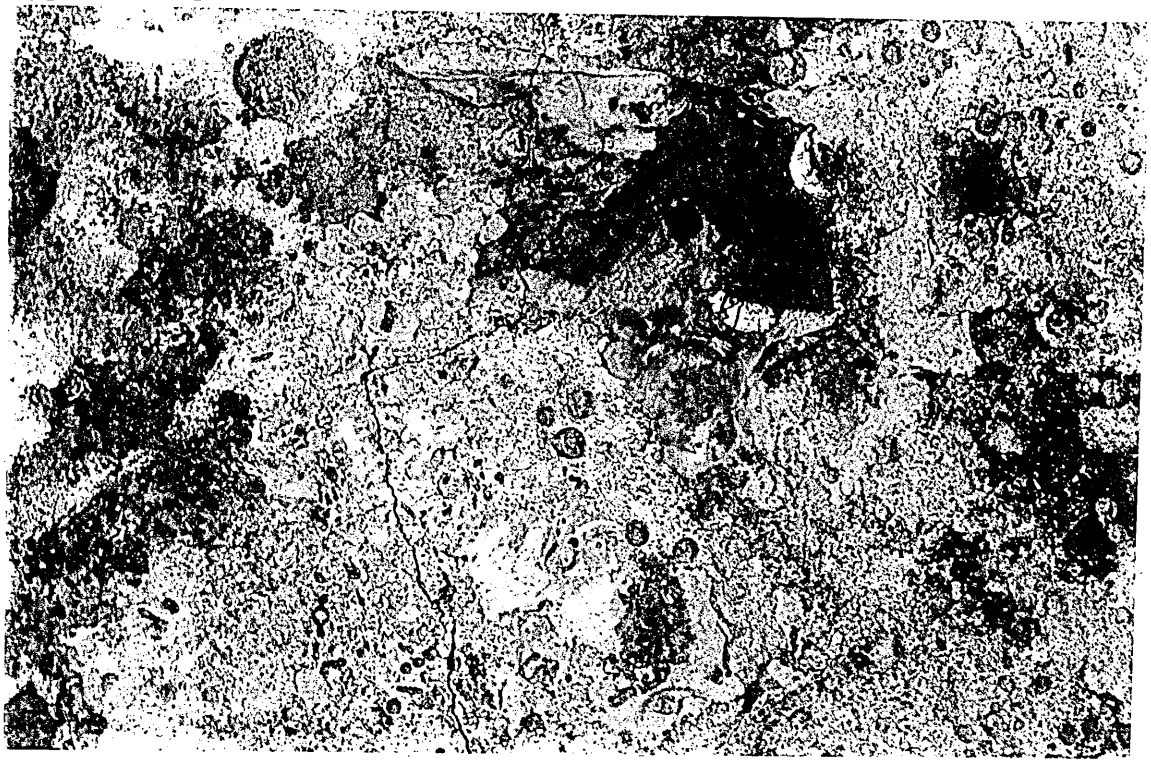


Figure 5.16: Right valve of *'Eopecten B'*. Remaining shell material largely restricted to borings. Specimen BB6/90. Note long straight hinge line. Width of field of view = 120mm.

The second morphological type is less well preserved and supplies less information than type A. The right valves of these specimens are of similar valve height and shape, being ovoid with a straight hinge line. The valve is totally flat with no sign of 'lift-off' and would seem to have been either cemented or tightly adpressed to the substrate for the entire ontogeny. The outer shell layers clearly follow the irregularities in the substrate with a high degree of accuracy; most of the visible shell material in BB6/90, which has been very badly abraded, is confined to that within borings in the original hardground surface (see figure 5.16). As before, details of the inner surface of the valve have been lost by diagenetic dissolution of shell material,

presumably aragonite. The outer calcitic shell layers which remain are very thin, mostly less than 2mm in thickness. Details of the external valve ornament are visible through this layer as fine (0.5mm) sinuous ribs radiating from the umbo. Umbonal angle (BB6/90)=115°. Elongate hinge line. The anterior auricle is very well developed. The byssal notch is deep, with no ctenolium observed. The byssal notch appears to remain open with no specimens developing an occluding fasciole.
The preserved shell structure is identical to that seen in Type A.

Both of the above descriptions pertain only to the 'lower' (right) valves. No certain left valve was identified in the field. However, a single specimen was observed, but not collected, in the Carrière des Campagnettes which may have been a left valve. The specimen, illustrated in Figure 5.17 was ovoid with a valve height of 140mm, with a straight hinge line and apparently had a calcitic outer shell layer and aragonitic inner shell layers, the latter now lost by dissolution. The general absence of left valves may perhaps be explained by the fact that these bivalves are preserved as hardground faunas and that the free valves were transported away. However, the fact remains that putative left valves have not been discovered in any other beds of similar age found locally.

Figure 5.17: Putative left valve. Carrière des Campagnettes. Lense cap=67mm diameter.

How do morphologies A and B relate?

The stratigraphical and geographical co-occurrence of these two morphologies of large cementing pectinids is strongly suggestive that the two are related. The only major difference between the two morphs is in the thickness of the valves and the failure of Type B to occlude the byssal notch despite being cemented. A solution to the latter problem is that maybe Type B did occlude the notch but by using aragonitic shell material, subsequently lost by dissolution. This is regarded as unlikely as all other cementing pectinids, including Type A, utilise calcite for the fasciole.

A scenario which covers both differences between valves is as follows. Initial ventral growth was rapid, producing a thin shell pectinid (i.e. Type B). Having attained a valve height of around 170mm further shell secretion was restricted to increasing the thickness of the valves. Such a growth pattern may be an adaptive strategy for rapid colonization of a limited substratum in competition with other epibionts. If such a scenario were correct then we might expect to find confirmation of this in the growth lines. The anticipated form of these growth lines is illustrated in Figure 5.18. However, as yet acetate peels have failed to pick out growth lines in sufficient detail either to accept or reject this hypothesis.

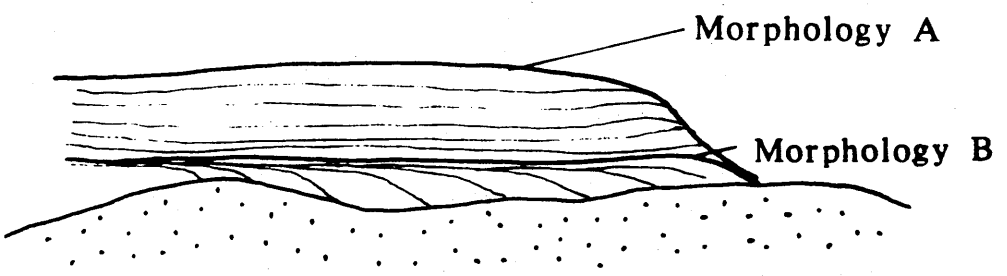


Figure 5.18: Hypothetical relationship between the morphologies of '*Eopecten*' Type A and B. Fine lines represent growth lines.

5.2.4.3 Palaeoecology

It is possible to reconstruct the life habit and the changes during ontogeny of these bivalves. Up to a valve height of around 44mm the organism was clearly byssally

attached, lying pleurothetically on the right valve. The presence of a ctenolium indicates, according to Waller (1984), that the attachment is tight. Cementation by the right valve followed and continued for a variable amount of time. It is likely that the extent of attachment, prior to 'lift off', was at least in part governed by the availability of the substrate. For example BB1/90, which is attached to a block of flat hardground, shows no sign of lift off despite having attained a valve height of 175mm.

From the field evidence on the foreshore at Luc it is probable that this bivalve was reasonably gregarious on the sea floor and that successive generations even used their predecessors as substrates.

5.2.4.4 Identification

Study of the literature on faunas from the relevant ages and areas, such as Arkell (1927-1931), Deslongchamps (1860, 1864), Dechaseux (1936), Buckman (1893) and Morris and Lycett (1853) has failed to reveal any published figure or mention of these bivalves. It is puzzling that such a geologically well known area as the Middle Jurassic of Britain and France should only now yield such unknown fossils. Yet the same was recently true for *Eonomia* described by Fürsich and Palmer (1982). There are perhaps two factors which account for this; either these bivalves have been mistaken for oysters, an error which may be understandable in beds where the large *Liostrea wiltonensis* is found, or they were noticed but not recovered due to the fact that their presence on hardground surfaces defies ready collection.

This Middle Jurassic bivalve is obviously of the superfamily Pectinacea, with its clearly defined disc, long straight hinge line, dextrally pleurothetic habit and radial sculpture. According to Waller (1984), the presence of the ctenolium, at least in type A, indicates membership of the Pectinidae. The presence of prismatic outer layers only in the earliest phases is also the typical shell microstructure for the family (Waller, 1972).

A careful study has been made of Jurassic pectinids in the collections of NHP, SD, BCM and OUM (these were considered to be the museums in which it was most likely

that comparable material would be found). This search had two purposes; to discover further examples from previously collected material and to gain an impression of possible relationships with previously described taxa.

(i) No direct analogues of specimens of Type A morphology were found. However specimens very similar to those of Type B were located. Sedgwick specimens J53837 *Velata tegulata* (Morris and Lycett), J707-8 and J4193 *V. anglica* (Arkell) and J53837-9 *Eopecten abjectus* (Phillips) all appear attached and analogous to the Type B Normandy specimens. All have open byssal notches and ctenolia. A further two unnumbered specimens from BCM, labelled *Hinnites* and collected in 1835 from the Inferior Oolite at Dundry were identified but did not appear to have cemented. A further uncemented specimen of *Velata abjectus* , in NHP specimen 65949 collected from the nearby Les Moutiers, described in the next section, is also remarkably similar.

An additional specimen of a right valve, described by Arkell (1931) as *V. wiltonensis* (Arkell) but regarded by Johnson (1984) as *E. spondyloides* is deposited in Devizes Museum. This specimen has been observed by TJP who confirms that, although uncemented, it closely resembles those collected from Normandy.

(ii) The most promising candidate for similarity within the previously described pectinids is *Eopecten (Velata)*. *Eopecten* is an enigmatic genus known almost exclusively from left valves ranging from the Lower Jurassic (Hettangian) to the Lower Cretaceous (Albian). In the *Treatise,* Hertlein places the genus in his uncertain group within the Pectinidae. Although he indicates that the bivalve attaches by the umbo, his description is dubious and does not tally with those of other authors. The generic name *Velata* given by Quenstedt in 1856, is preoccupied by the gastropod *Velates* (Montfort). Although Phillipi emended the offending name to *Velopecten* in 1898, his pronouncement was pre-dated by Douvillé's description of the genus as *Eopecten* (1897). Arkell (1931) and Cox (1928, 1942) argue for the retention of *Velata,* suggesting it valid. However, my understanding of nomenclatural procedures

suggests that this is not so and that Douvillé's *Eopecten* is correct, an interpretation which concurs with that of Johnson (1984).

It is Johnson (1984) who provides the most thorough account of the genus. He recognises the genus to be subject to a great amount of variation, much of it ecophenotypic, a fact which allowed him to synonymise the immense number of previously described species into a mere three; *Eopecten velatus* (Goldfuss), *E. abjectus* (Phillips) and *E. spondyloides* (Roemer). There is a marked similarity between the *Eopecten* described by Johnson and the large Normandy pectinid, in particular those of morphology B. The major discrepancy, however, lies in the reported life habit. Johnson (1984 and personal communication) states emphatically that *Eopecten* did not cement. Cox (1942) also made a specific enquiry into the life habit of the genus but found no conclusive evidence to support cementation.

Did Eopecten cement?

All specimens housed in the museums listed above which were labelled *Eopecten, Velata, Velopecten* or *Hinnites* (of Jurassic age) were inspected for evidence of cementation. There is a general paucity of right valves, for example there are 263 specimens in the NHP which purport to be of *Eopecten* of which only 6 are of right valves. This may be interpreted as suggestive that the genus did cement but cannot by itself be regarded as conclusive. As described by Arkell (1931), Cox (1942) and Johnson (1984), the right valve, where present, is thin and 'puckered', mostly displaying fine sinuous ribbing - implying perhaps conformity to an irregular substratum.

Most specimens examined support the view that *Eopecten* was byssally attached and may be exemplified by NHP 65949. This large specimen, of valve height 150mm, is labelled *Velata abjectus* and was collected from the Bajocian at Les Moutiers in Calvados, France. The specimen is complete, with both valves being present. The right valve is thin with fine straight ribbing and with a deep open byssal notch and a functional ctenolium. The valve is virtually flat except for a slight concavity, probably

due to substrate influence (possibly the inside of another bivalve). It is akin to morphology B.

Several of the left valves examined display xenomorphism, e.g. SD B11649 *Velata anglica*, a fact suggested by Cox (1942) that may signal cementation. However, Johnson (1984) cites a personal communication from Seilacher which states that the xenomorphic ornament of *Eopecten* is poor and that this is due to movement on the byssus, i.e. positive evidence against cementation. However, in Section 4.4.2.1. I have drawn the conclusion that the precision of xenomorphic ornament is to a large extent inversely correlated with the thickness of the mantle margins. By analogy with modern pectinids it may be inferred that *Eopecten* had a well developed middle mantle margin complete with sensory tentacles and ocelli, and therefore one would predict that its capacity for precise xenomorphism would have been low. On these grounds I would regard Seilacher's evidence as equivocal.

Although NHP LL10979 *Velata anglica*, collected from the Corallian of Dorset , lies in close proximity to an *Isognomon* there is clearly matrix between them. The only positive evidence for *Eopecten* cementing is from the Sedgwick specimens mentioned earlier. Although Johnson visited the Sedgwick it is not recorded what he deduced from these specimens.

Is the Normandy pectinid Eopecten?

It is difficult to marry the valves of a bivalve known only from its right valve with those of a genus known almost exclusively from the left. However my tentative conclusions are that the similarities between *Eopecten* and the Normandy pectinids, in particular those of morphology B, is marked enough to consider them the same genus. Yet there is a marked difference in size between the specimens. Johnson (1984) reports maximum valve heights for *Eopecten* of around 110mm- considerably shorter than the Normandy specimens. Another problem with this identification is the distinct lack of left valves of this genus in any of the Normandy deposits. Apart from a fragment of a small specimen of *Eopecten* found by J.Todd at the Carrière des Campagnettes no others have been found. Palmer (1974) records the genus as rare.

If this cementer truly does belong to *Eopecten* it raises some interesting implications for the genus. Of the few right valves which were previously known, most, e.g. NHP 65949, were unquestionably byssally attached. The implication of this is that only certain species within the genus have the ability to cement, or alternatively that, like *Chlamys pusio*, *Eopecten* cemented facultatively.

5.3 HOW WELL PREADAPTED IS THE FAMILY PECTINIDAE FOR CEMENTATION?

Byssate attachment is the primitive condition in the Pectinidae, from which both the cemented and free lying /swimming habits have been derived. The preceding sections show that cementation has evolved in the family at least four times, over geological time. This may be a conservative estimate. Apparently cementing pectinids such as *Pecten ercolaianus* figured by Glibert (1945, Plate 3, figure 8a and b), and '*Hinnites* ' *pasca*, supposedly endemic to Easter Island (Rehder, 1980), have gone uninvestigated in this thesis. Nevertheless the picture is one of a highly preadapted family in which cementation may evolve with relative ease.

Following the layout of Chapter 4, this section looks at the preadaptations for cementation which the family as a whole possess which have enabled them to exploit the cemented habit.

All pectinids are pleurothetic. As established in Section 4.2.1, this condition, which inevitably leads to the mantle margins lying in close proximity to a substrate, is a useful, although not paramount, preadaptation. Byssate attachment, at least in early ontogenetic stages, maintains this substratal contact. Many of these forms, for example *Chlamys varia,* are distorted by substratum topography despite not being actually cemented to it.

Certain pectinids have a much more intimate association with potential substrates. *Hemipecten forbesianus* is noted for its extremely tight byssal fixation, (Yonge, 1981), to the extent that Douvillé (1897) erroneously supposed it cemented. What is

particularly interesting about this bivalve is the deeply embayed byssal notch and Yonge's (1981) observation that the byssal threads possibly terminated with calcareous material. This implies a possible convergence with the anomiids. *Pedum spondyloideum* lives, attached by a byssus, enclosed within scleractinian corals. Although this association is with the living coral, Yonge (1967a) notes that the presence of the bivalve killed the surrounding polyps. This effectively sheaths the bivalve in hard substratum. Commensal relationships with sponges are also common, e.g. *Chlamys dieffenbachi* (Beu, 1965) and *C.varia* (Forester, 1979). The former species displays a polymorphism; individuals associated with sponges being spinose whilst the rarer unenclosed morphs lack spines (Beu, 1965). The type material of *C.dieffenbachi* held at NHZ is clearly distorted. However Beu (personal communication) stresses that no cementation occurs. These examples of pectinids which live in exceedingly close proximity to substrates are a very short step away from actually adhering to them. Only minor modification to the shell secreting processes will allow such adhesion.

As a family, the Pectinidae possess all the key preadaptations for cementation recognised in Chapter 4. The mantle margins are highly extensible and are attached at a dorsally inset pallial line. Example mean IR values (derived from data given in Appendix 3) are *Chlamys varia* (byssate)=0.26, *Chlamys pusio* (cemented)=0.35 and *Pecten maximus* (free)=0.33. As suggested previously, this dorsal inset of the pallial line is probably a consequence of a flattened shape and possession of a well developed middle mantle lobe and its requirement to be retracted deep within the valves. Thayer (1972) in his investigation into the swimming Monomyaria remarks upon the well inset pallial line of the pectinids, correlating it with small body size which he believes to be an adaptation to swimming.

The Pectinidae are also all possessors of an exceedingly thin periostracum (see Table 3.2), none with a thickness exceeding 1μm. Again students of swimming pectinids believe this to be a vital preadaptation for that habit, (Moore and Trueman, 1971).

The conclusion of this section is that the entire Family Pectinidae possess the major preadaptations for the evolution of the cemented habit. It is clear that only minor modification of the character of the periostracum is required in order to allow the leakage of extrapallial fluid. However, despite its polyphyletic acquisition within the family, cementation has occurred only sporadically in low taxonomic units and has not become widespread throughout the family. Certainly the cementing pectinids have never approached the success of other cementing clades, such as the rudists or oysters. Nevertheless the repeated evolution of the habit from a well preadapted group has great potential in actually detecting the circumstances favouring the evolution of cementation.

5.4 CONCLUSIONS

1]. Cementation has arisen polyphyletically in the Pectinidae. Four clades are identified here, *Hinnites, Prohinnites, Chlamys pusio* and *Eopecten.*

2]. *Crassadoma* Bernard is a synonym of *Hinnites.*

3]. *Chlamys pusio* is a facultative cementer in which the ability to cement has been acquired since the Pleistocene.

4]. A large cementing pectinid from the Middle Jurassic of Normandy and England is tentatively placed within the genus *Eopecten.* The life habits of this genus have previously been regarded as enigmatic.

5]. The Pectinidae possess the major preadaptations for cementation, thus facilitating the multiple acquisition of the habit.

CHAPTER 6

THE ROLE OF PREDATION IN THE EVOLUTION OF THE CEMENTED HABIT - AN EXPERIMENTAL INVESTIGATION

".....there is no compelling necessity to become shell cemented."

Nicol (1978)

6.1 INTRODUCTION

Cementation is an extreme life habit. Most exponents become irreversibly attached, although a few exceptions such as *Spondylus imperialis* and *Echinochama arcinella* do gain secondary freedom. The remainder are condemned to live at the site on which cementation first occurred, in the case of *Ostrea edulis* selected merely 10-15 days after fertilization (Waller 1981).

Epifaunal attachment by bivalves may alternatively be achieved by byssal threads. Chapter 4 surveys the evidence that most, if not all, cementers evolved from byssate ancestors. This raises the important question: Why cement ? What are the selection pressures which favour cementation over byssal attachment ?

6.2 BYSSAL ATTACHMENT vs CEMENTATION

The byssate habit in the Bivalvia is widespread. Yonge (1962b) suggests that probably all bivalves possess a byssus in their juvenile stages and that this has been neotenously retained in the adults of certain groups. He lists twelve superfamilies which have representatives with an adult byssus. Chapter 2 enumerates at least 20

independent occurrences of the cemented habit and yet I perceive a number of advantages that byssal attachment has over the cemented habit. These are as follows:

1] Cemented bivalves are unable to reattach if dislodged, for example by excessive wave force or an unsuccessful predation attempt. A growing edge of the fixed valve may lift off and reattach, as with *Spondylus aurantius* NHZ 40.1 19.39, if the initial attachment is maintained. Presumably the ability to reattach depends on whether the periostracal groove can be re-applied to the substratum. In his study of *Spondylus americanus* Logan (1974) found that some were lying free having been detached in storm conditions. He indicated that these were cast into unfavourable orientations and locations and were unlikely to survive long. In contrast byssate bivalves such as *Mytilus edulis* and *Chlamys varia* can rapidly produce new byssal threads if dislodged and regain attachment to the substratum.

2] Related to the above, is the ability of byssate bivalves to cast off voluntarily, move and reattach. This has obvious advantages where environmental conditions become undesirable. Bayne (1964) describes primary and secondary settlement in *Mytilus edulis*. After a planktonic phase, the plantigrades settle on filamentous algae or hydroids for thirty days before detaching and migrating to the adult mussel beds. Bayne argues that this is an adaptation to avoid competition with the adults and the dangers of being inhaled by the adults' siphons. The sea scallop, *Placopecten magellanicus*, also shows juvenile settling away from the mature individuals and an alternating habit in the adult between free swimming and byssal attachment (Caddy 1972). Paine (1971) attributes the success of the mytilid *Perna canaliculus* to its ability to sever its byssus and move. In addition I have evidence that *Mytilus* can migrate without total detachment; individuals held in an aquarium were observed climbing vertically up the glass.

Cemented bivalves have no such ability to sunder voluntarily and reattach.

3] A flexible attachment facilitates withstanding wave surge. Waite (1983) notes that the flexibility of byssal threads dissipates wave energy. Smeathers and Vincent (1979) show that the byssus of the mussel is adapted for massive shock absorbance and calculate that only fifty threads are sufficient to withstand all but the most severe winter storms. By contrast the cemented forms offer a rigid resistance to wave force and are thus liable to be knocked off (Feifarek, 1987 and Logan, 1974). It should be noted here that rigid fixation is far less of a problem in smaller encrusting forms such as barnacles and bryozoa, which tend to lie within the boundary zone, thus protected from the highest water velocities. There is also fair evidence that these forms do use an organic glue to attach, which will be more shock absorbant than a totally rigid attachment.

4] The strength of cemented attachment cannot be varied. Price (1982) describes the seasonal variation of the byssal attachment in *Mytilus edulis*, with maximum strength coinciding with the winter storms, and the weakest with the summer months. Hepburn et al. (1979) report that low turbulence communities of mussels produce fewer byssal threads than those in more vigorous environments.

5] Byssate bivalves flourish at all latitudes, whereas cementers are confined to lower latitudes, (see Section 2.4.3 and Nicol, 1964). This may be in part due to the physical problems of producing a calcareous cement with the increased solubility of calcium carbonate in lower water temperatures, (see Chapter 4). There are no such problems in producing proteinaceous strands in cool temperatures.

6] *Mytilus edulis* may also utilise byssal threads as a novel defence against predation. Carriker (1980) and Petraitis (1987) record, respectively, *Urosalpinx cinerea* and *Nucella lapillus* being immobilised by byssal threads of their mussel prey.

6.3 WHY CEMENT?

Clearly the multiple acquisition of the cemented habit in independent clades of byssate bivalves is not accidental and definite selection pressures must favour its evolution.

6.3.1.1 Traditional views

Most authors recognise cementation as an advanced life habit e.g. Kauffman (in Moore, 1969), Stanley (1970), Nicol (1978), and Yonge (1979), and yet few have critically examined the selection pressures that favour its acquisition. Nicol (1978) is convinced of the superiority of byssal attachment and can see "no compelling necessity to become shell cemented". Apart from this single doubt the view that cementation is an adaptation to life in a turbulent environment is entrenched in the literature. For example, Kauffman (in Moore, 1969) states "the primary function of this [cemented] habit is obvious; it provides continued stable orientation in the preferred habitat...of high energy wave and current conditions.". However, there is no real evidence for this.

6.3.1.2 Criticism

(i) Cemented bivalves do frequently inhabit high energy conditions. It is also true that cemented bivalves require a clean, hard substratum on which to attach. These two facts indicate a certain circularity to the Kauffman argument; in many instances the exacting substrate requirements will only be met in energy conditions likely to produce sediment free surfaces, and successful spat settlement will be *restricted* to these areas. Elsewhere, in low energy, soft bottom conditions, colonisation by cementing bivalves is only possible by encrustation of hard 'islands' e.g. *Echinocorys* tests in the Chalk (Hammond, 1988). I suspect that the limitation of *Etheria* to the rapids of African river systems reported by Pilsbury and Bequaert (1927) is due to these areas being the only sites free enough from silt to allow encrustaion and to avoid subsequent burial.

(ii) Field evidence collected on the west coast of Eire in 1988 shows the success of byssate *Mytilus edulis* on exposed shores. Finnavara Point , County Clare, juts out into Galway Bay (Figure 6.1a) such that the north side is exposed to the waves

coming from the Atlantic, whereas the southern side is more sheltered. The malacofauna of the point was surveyed (Figure 6.1b), revealing that although *Mytilus* was found over the entirety of the surveyed area, it appeared in isolation on the most exposed portion of the northern side. On the sheltered sandy southern side the mussels occurred in conjunction with the cementers *Ostrea edulis, Chlamys pusio* and *Anomia ephippium*, along with byssally attached *Arca tetragona* and *Chlamys varia*. It is also important to note in the light of the sections to come that the exposed areas were conspicuously lacking in the predators *Asterias rubens, Nucella lapillus, Buccinum undatum* and *Carcinus maenas*, which were however abundant on the sheltered side.

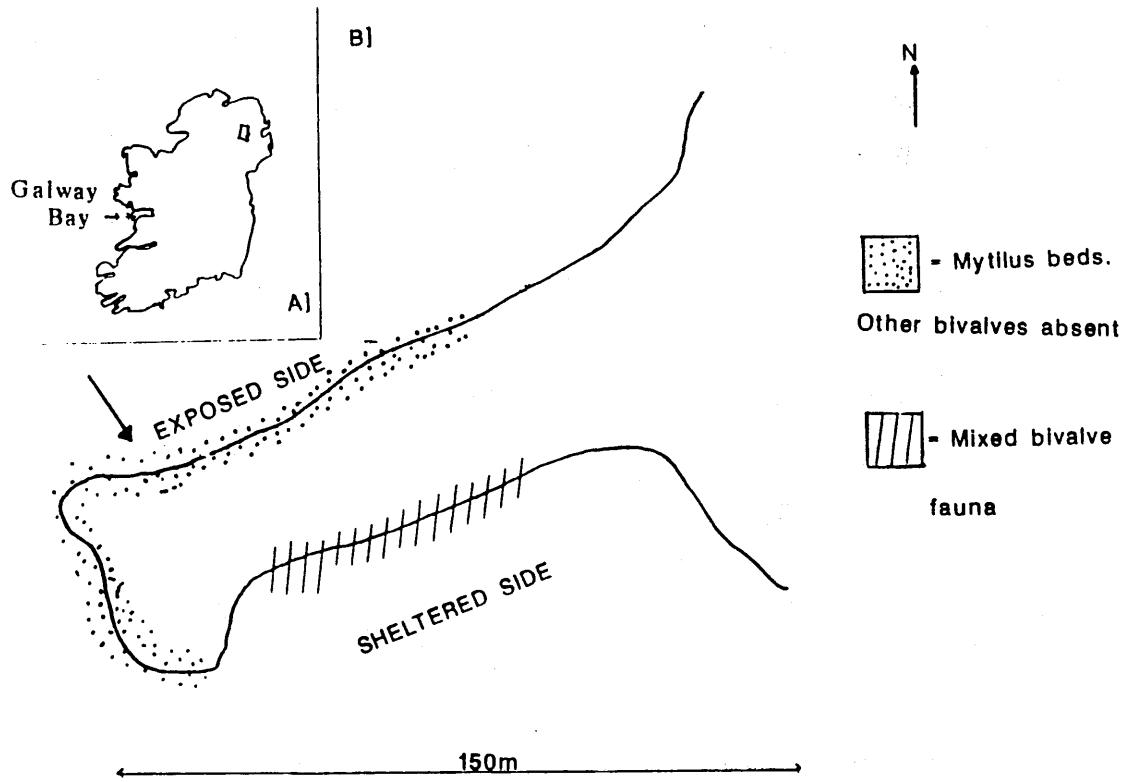


Figure 6.1: a) Location map of Finnavara Point in Galway Bay. b) The distribution of epifaunal bivalves surveyed on the Point at the Low Spring tides April 1988.

Other authors have also noted the dominance of *Mytilus* in high energy conditions, e.g. Kitching, Sloane and Ebling (1959), whilst Yonge (1974) describes the following byssate bivalves from the high energy zones of reefs: Arcacea, Mytilacea, Carditacea, Pteriacea, Pectinidae and Tridacnidae.

(iii) Various attempts have been made to assess the relative strengths of bivalve attachment (e.g. Harger 1970, Waite 1983). A study of the adhesive strengths of various biofouling organisms by Udhayakumar and Karande (1986) reveals that the break loading of the byssal threads of *Mytilus edulis* is higher than that for the cemented shell of *Crassostrea cucullata.*

(iv) Points 1, 3 and 4 made in section 6.2, as advantages of the byssate over the cemented habit are also germane to living in a turbulent environment.

(v) The timing of the first appearances of the cemented habit in each of the clades specified in 2.3.3 is striking (Figure 6.2). Two main points are apparent:

- with the exception of the pseudomonotids the cemented habit is a post-Palaeozoic innovation.

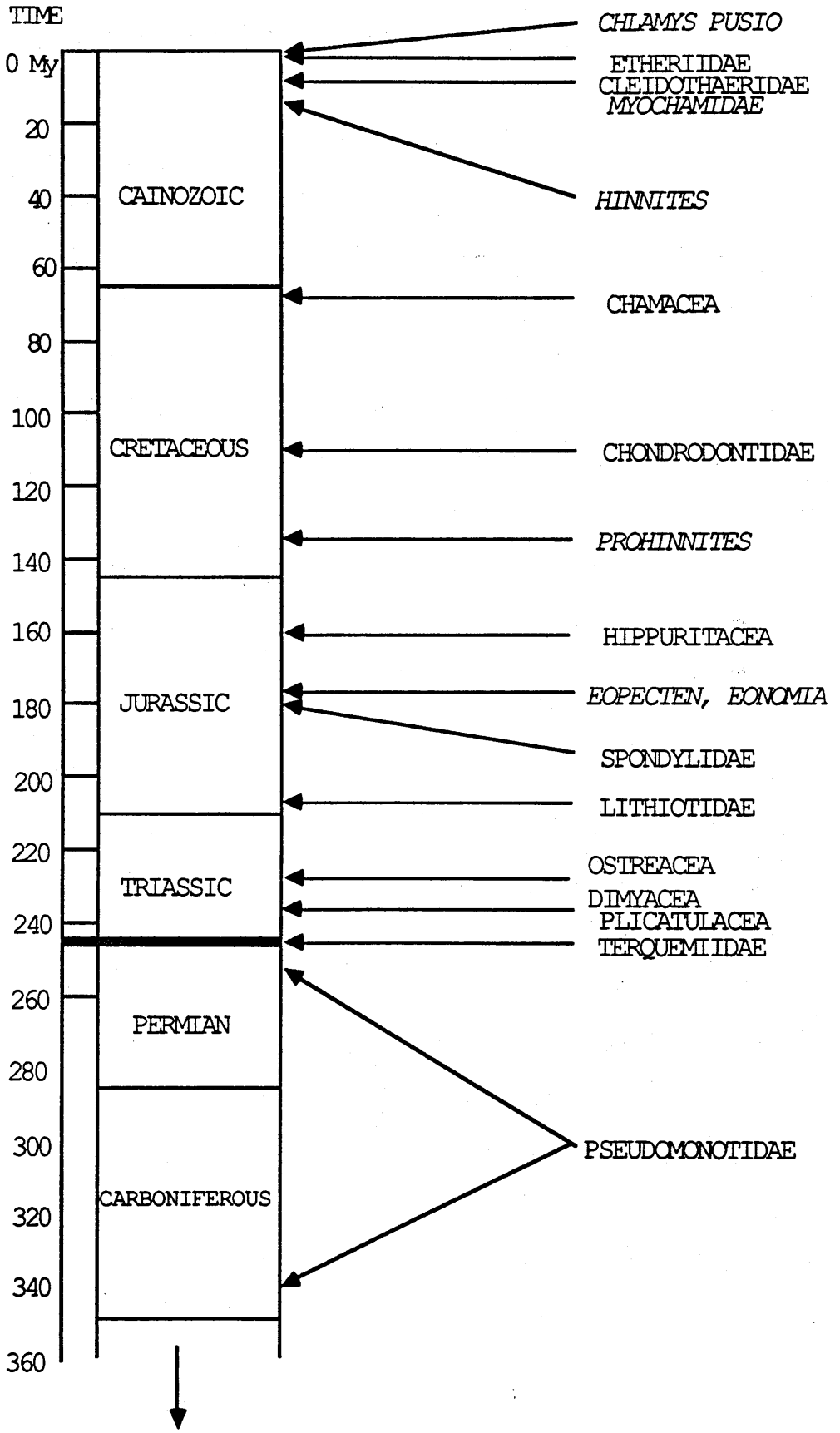


Figure 6.2: Temporal distribution of the first appearances of each of the cemented clades recognised in Chapter 2. Data culled from Chapter 2.

- The Early Mesozoic is a key time for the evolution of the habit. The oysters, plicatulids, dimyids, lithiotids, terquemiids and spondylids all independently acquire the habit during the Triassic and Jurassic.

Palmer and Palmer (1977) describe the encrusting fauna of a middle Ordovician hardground of echinoderms and bryozoans. Although these taxa dominate Palaeozoic hardground communities, encrustational life habits had also been evolved by the Palaeozoic brachiopods, sponges, corals and serpulids. In the case of the brachiopods, the cemented habit was independently evolved five times in the Palaeozoic (Rudwick, 1970). Clearly there was no shortage of available Palaeozoic hard substrata for encrustation, and reason enough for other taxa to evolve a cemented habit. Although one might expect the specialist requirements for cementation in the bivalves (see Chapters 3 and 4) to be gained and exploited 'late' in the group's evolutionary history, one would not expect them to be acquired over such a short period of geological time in so many clades.

Although firm attachment to a hard substratum is advantageous to life in a high energy environment, there are serious disadvantages to the irrevocable attachment of cementation. In many cases byssal attachment provides both stronger and more flexible attachment with the advantages of mobility. It is therefore necessary that we seek elsewhere for an alternative selection pressure which favours the acquisition of the cemented habit in the bivalves.

6.3.2 New proposal

The search for an alternative must encompass both changes in the physical and biotic environment.

Physical

There is no evidence that there was any sudden increase in the availability of hard substrata at the beginning of the Mesozoic. Nor is there any indication that there was

an increase in overall water movement which might favour a 'sudden' widespread adaptation to cement. The only physical change occurring at the Palaeozoic/Mesozoic boundary, which might possibly have influenced the acquisition of the cemented habit, would seem to be the changes in CO_2 level inferred by Sandberg (1983). As discussed in 4.5.1, this change is liable to have facilitated the cementation process in those clades preadapted for the habit, but this cannot be seen as a selection pressure that would favour the cemented over the byssate habit.

Biotic

Possible biotic explanations hinge on the massive reorganization of marine communities which followed the Permian/Triassic extinctions. The brachiopods figured highly amongst the casualities of the mass extinctions, including many of the cementing clades; the davidsoniaceans, strophalosiaceans and the richthofeniids. Did these extinctions release the niches for the cementing bivalves to exploit ? It is tempting to envisage the cementing brachiopods taking their final bow with the preadapted ancestors of the cementing bivalves waiting impatiently in the wings. Such an engaging scenario is, however, unlikely; as discussed in Chapter 7, the cemented habit in the brachiopods was developed in only a limited and sporadic way, never seeming to gain any advantage over the pedunculates. Rudwick (1970) states "Ecologically a cemented brachiopod would be at a disadvantage to one attached by a pedicle..". Although the richthofeniids were capable of 'reef' building, it is unlikely that the niches vacated by the cementing brachiopods were very large or diverse.

The biotic change that did occur at this time, with the potential of having a profound effect on the evolution of epifaunal organisms, was the Mesozoic Marine Revolution (MMR). The concept of this sudden appearance and subsequent diversification thereafter of many predator groups has been extensively documented by Vermeij (1977,1978, and 1987).

6.3.3 A role for predation in the evolution of the cemented habit ?

6.3.3.1 The MMR and molluscivory

Table 6.1 Major molluscivorous groups: feeding methods and first appearance dates of the habit.

PREDATORY GROUP	FEEDING METHOD	FIRST APPEARANCE	COMMENTS
Asteroidea	Extraoral - eversion of the stomach lobes through the mouth into or around the prey.	Triassic/early Jurassic (Blake (1981) and Gale (1987))	Carter (1968) cites Clarke (1912) as evidence that the extraoral habit was evolved by the Ordovician. However Gale (1987) demonstrates that Palaeozoic asteroids lacked the fundamental requirements to feed in this manner i.e. appropriate musculature, suckered tube feet, and a flexible mouth frame to enable stomach eversion.
Crustacea -Brachyurans -Stomatopods	Crushing, chipping Hammering, spearing (Methods reviewed by Lau (1987)).	Pliensbachian Late Jurassic	Potentially shell breaking crustaceans had evolved by the Palaeozoic, but there is no direct evidence for this habit in the fossil record (Vermeij 1987).
Gastropoda -Buccinidae -Naticidae -Muricidae	Wedging Drilling Drilling	Barremian Albian Albian	Details from Taylor et al. (1980) and Taylor et al. (1983). Fürsich and Jablonski (1984) note Triassic naticid-like drill holes claiming that the ability to drill in naticids had evolved at this time but failed to radiate, although Carriker and Yochelson (1968) regard Palaeozoic drill holes as products of post mortem scavenging.

Cephalopoda Nautilioids Octopods	Crushing Drilling	?Ordovician Ladinian Mid. Jurassic	Alexander (1981) and Peel (1984) both attribute Palaeozoic damage to brachiopods and gastropods to cephalopods but the evidence is equivocal.
Fish -Chondrichthyes -Placoderms -Dipnoans -Pycnodontiforms -Seminotiforms -Batoids (rays and skates) -Heterodontid sharks -Actinopterygii	 Crushing Crushing Crushing Crushing Crushing Crushing Crushing Crushing	 Early Carboniferous Devonian Devonian Late Triassic Late Triassic Early Jurassic Early Jurassic Early Cainozoic	 Fresh water only Massive radiation thereafter
Reptiles	Crushing	Triassic	First demonstrable molluscivores were placodonts (Vermeij, 1987). Diversification thereafter
Birds	Spearing and hammering	Neogene (Carter 1968)	Variety of waders, gulls and ducks etc.
Mammals	Crushing	Miocene	e.g. pinnipedes, otters etc.

Table 6.1 indicates the major molluscivorous groups, their methods of predation and their geological range. Material is drawn largely from the work of Carter (1968), Vermeij (1987) and from personal observations.

Vermeij (1987) catalogues the rise of all predatory groups over geological time. The earliest signs of predation in the Early Cambrian, evidence of drilling and repair in the enigmatic *Morbegella* sp. (Bengtson, 1968), precedes any evidence of molluscivory. The first demonstrable evidence of attacks on molluscs come from the Devonian, with only the fishes and possibly cephalopods as putative culprits. Vermeij finds no evidence that the Palaeozoic arthropods fed on live molluscs.

The beginning of the Mesozoic heralded a spectacular increase and diversification of the molluscivorous habit. The most voracious of modern molluscivores, the asteroids, the crustaceans and the drilling naticid and muricid gastropods, all evolved the habit within the Mesozoic, the former two originating in the early part of the era.

Inspection of Table 6.1 reveals that the early Mesozoic was a key time in the appearance of the molluscivorous habit.

6.3.3.2 Temporal considerations

Figure 6.3 plots first appearance data from Table 6.1 together with the data given in Figure 6.2 (first appearance of the cemented clades of bivalves). There is a striking temporal coincidence between the evolution of molluscivory and that of cementation.

Vermeij's classic paper of 1977 describes the changing trends in gastropod morphology since the Mesozoic, towards increased external ornament, narrow elongate apertures and closed coiling. These changes he interprets as defensive adaptations in response to the MMR.

Is predation pressure likely to be an effective selection agent on epifaunal bivalves? Vermeij (1983) indicates that marginal damage to bivalved animals is more critical than it is to gastropods. Bivalves which suffer marginal damage in a failed predation attempt are more likely to attract further predation, and, in the case of intertidal species, also risk death by desiccation. Thus Vermeij suggests that the bivalve response to predation pressures is by escape and avoidance rather than increase in armour. From this one can conclude that the epifaunal bivalves, particularly those which attach, will be susceptible to predation pressure as a selective agent. Hence the MMR must have been a critical time in bivalve evolution.

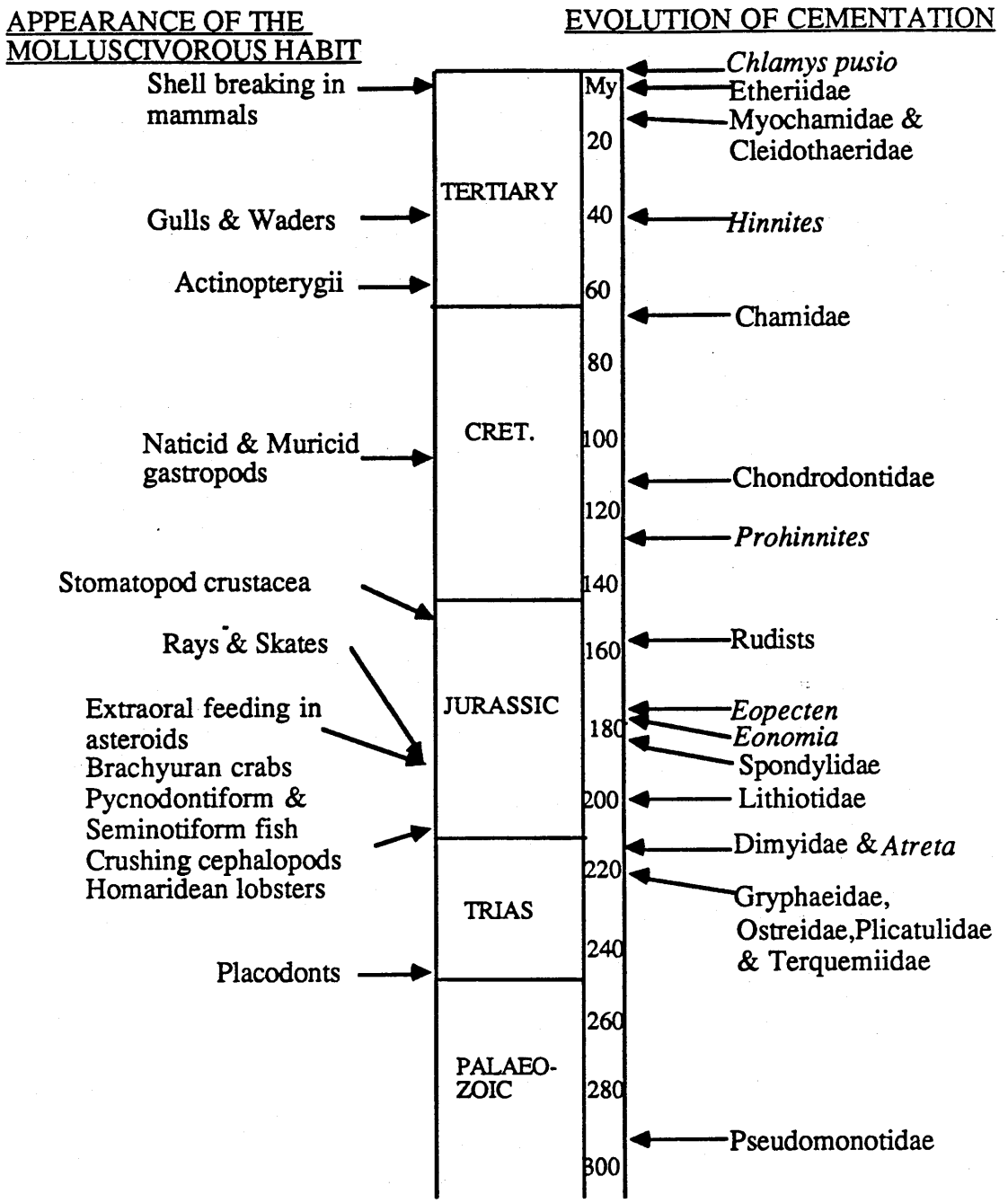


Figure 6.3: Temporal distribution for the first appearances of the cemented clades and the molluscivorous habit.

6.3.3.3 Experimental investigation

The relative susceptibility of byssate and cemented bivalves to predation has been experimentally tested:

6.3.3.3.1 The experimental theory and null hypothesis

The basic experiment was to offer predators a choice between byssate and cemented bivalve prey. A null hypothesis (H0), was proposed, stating that byssally attached and cemented bivalves are equally vulnerable to predation. Therefore predators would express no preference between the two prey types, all other parameters being equal; and hence the relative numbers eaten will be directly proportional to their relative abundance i.e. encounter rate.

6.3.3.3.2 Experimental procedures

These experiments, based upon prototypes designed in aquaria at the OU, were run at Dunstaffnage Marine Laboratories (SMBA) near Oban over three experimental periods lasting in total two and a half months.

Prey

In order that the only difference between prey items should be the mode of attachment, a single prey species was used. This prevented the predator from choosing its prey on the basis of other factors, e.g calorific value or other defensive strategies, besides mode of attachment. The prey species selected was *Mytilus edulis*, collected intertidally in Dunstaffnage Bay.

Byssate prey Byssally attached *single* individuals were collected on their natural substrates, (Figure 6.4a).

Cemented prey Cementation was simulated by glueing one valve of the bivalve to large blocks of rock substrate with epoxy resin (Araldite rapid - Ciba Geigy), (Figure 6.4b). The angle of attachment was varied. Laboratory work prior to field trials showed that the epoxy resin was resistant to dissolution in seawater and, after curing, released no noxious byproducts toxic to marine animals. This 'cementation' did not affect the behaviour of the prey - after immersion all gaped normally and even spun

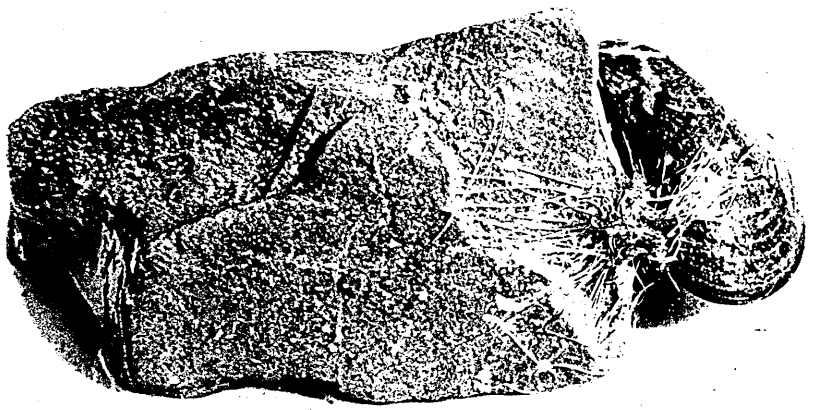


Figure 6.4a: Byssally attached prey. Retaken from colour slide.

Figure 6.4b: 'Cemented' prey. Retaken from colour slide.

superfluous byssal threads (see also Figure 6.4b). Specimens cemented in this way and returned to the shore were rediscovered 12 months later, still attached and living. The blocks of substrate used were in all cases large enough to prevent predator manipulation, thus avoiding treatment of the whole substrate as merely a large prey item.

The bivalves used varied in height from 10 to 55mm and were clear of all fouling epifauna. Only apparently healthy *Mytilus* were used. The strength of adduction out of water was tested by attempting to insert a fingernail between the valves - any which allowed entry were rejected. A sick mollusc, unable to adduct properly, will leak metabolites into the surrounding water, thus attracting predators, and will offer less resistance to attack. For the same reasons any individuals displaying marginal damage were also rejected.

In addition to the two basic prey categories a number of the byssate mussels were daubed with epoxy resin, in order to act as a control.

Predators

Predators were selected to fulfil the following criteria:

- voracious molluscivores with well known feeding biologies (see Table 6.2).
- collectable in Dunstaffnage Bay.
- having a recorded ability to consume both *Mytilus* and cemented bivalves.
- being adequately mobile, i.e. capable of finding many prey items.
- belonging to molluscivore groups which participated in the MMR.

The predators selected were the asteroid *Asterias rubens*, the crabs *Carcinus maenas*, *Cancer pagurus*, and the gastropods *Nucella lapillus* and *Buccinum undatum*. Their feeding methods are reviewed in Table 6.2. All were collected locally in Dunstaffnage Bay by SMBA divers, and were held in tanks without food for at least five days starvation prior to use. A range of sizes were used and all unhealthy individuals were discarded e.g. *Asterias* and crabs with missing limbs and *Carcinus maenas* parasitised by the cirripede *Sacculina carcini*. No sexual selection was made.

PREDATOR	FEEDING METHOD	REFERENCES
Asterias rubens	Extraoral	Lavoie (1956), Feder (1955)
Carcinus maenas	Crushing	Crothers (1968), Elner and Hughes (1978)
Cancer pagurus	Crushing	Lawton (1983)
Nucella lapillus	Drilling	Hughes and Drewett (1985)
Buccinum undatum	Wedging	Nielsen (1975)

Table 6.2 Predator groups used in the experiments, their predatory methods and the key references associated with them.

The predator groups used also have a wide latitudinal distribution. Although many authors regard asteroids as only important in higher temperate latitudes, e.g. Vermeij (personal communication), it should be noted that asteroids *do* have a predatory impact in the lower latitudes, for example the devastation of reefs by the crown of thorns starfish *Acanthaster planci* (Chesher, 1969).

The tank system

Experiments were run in outdoor tanks (1.5 X 0.8m), continually supplied by natural seawater running to waste. At all times the water temperatures exceeded 10°C. This system afforded the most natural conditions possible and was superior to caged experiments in the open sea for the following reasons:

- the tank system allowed constant monitoring and easy maintenance with minimal disturbance.
- conditions could be held constant and unwanted prey and predator individuals excluded. Several authors, e.g. Carriker (1951), report lost data sets owing to stray predators being attracted to and penetrating caged experiments.

All experiments were run in natural light, except those using *Carcinus*, which were kept in total darkness.

Figure 6.5 Tank set up. Retaken from colour slide.

The experiments were set up as simple choice chambers, see Figure 6.5. Table 6.3 shows the relative numbers of prey type and predator used in each experiment. Prey blocks were distributed randomly throughout the tank, to ensure a random encounter rate. In the majority of experiments the relative number of prey was held constant, any *Mytilus* which were eaten being replaced by similar specimens. No replacements were made in experiments 10 and 11.

Satiated predators were removed every three or four days and replaced with starved individuals.

EXPERIMENT NO.	PREDATOR	PREY: NUMBER BYSSATE	PREY: NUMBER CEMENTED
1	*Asterias*	25	25
2	*Asterias*	20	20
3	*Asterias*	25	25
4	*Cancer*	25	25
5	*Cancer*	20	20
6	*Carcinus*	25	25
7	Predator cocktail Ω	30	30
8	*Nucella*	20	20
9	*Buccinum*	20	20
10	*Asterias*∞	40	10
11	*Asterias*∞	10	40

Table 6.3 Details of experimental set up with the relative numbers of prey types offered. Ω denotes a mixture of *Asterias, Cancer* and *Carcinus* and ∞ denotes non replenishment experiments.

During the course of the experiments, detailed behavioural observations were made. Also the activity of predators in Experiment 3 were recorded every thirty minutes for two periods of seven and a half hours. In this way it was possible to assess the number of attempted and successful attacks.

6.3.3.3.3 Results

Table 6.4 gives the relative numbers of prey eaten in all experiments along with the numbers predicted by the null hypothesis. A third category of prey has been introduced to cover the 'cemented' individuals which were pulled off the substrates by the predator, probably due to failure to mix the epoxy correctly, insufficient curing time or failure of the substratum.

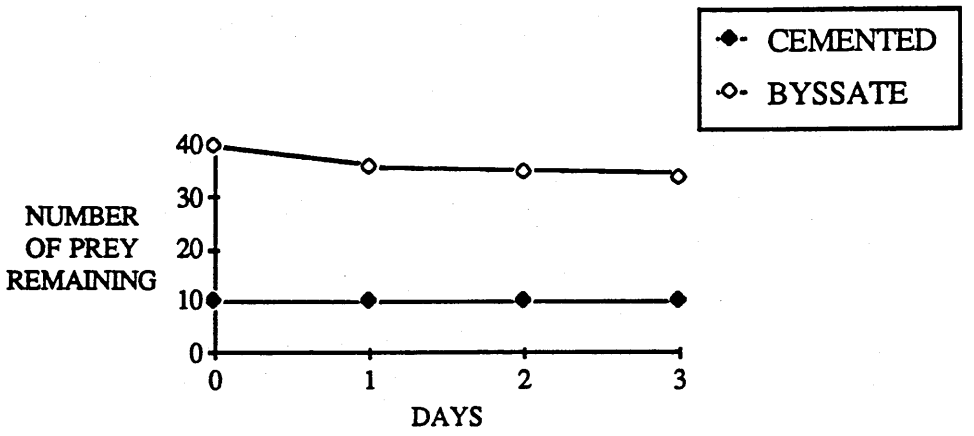
EXPERIMENT	NO. CEMENTED OBSERVED*	NO. CEMENTED EXPECTED	NO. BYSSATE OBSERVED	NO. BYSSATE EXPECTED
1	9(7)	20	31	20
2	7(4)	12	17	12
3	26(15)	60.5	95	60.5
4	36(7)	66	96	66
5	29(26)	45	61	45
6	8(4)	13.5	19	13.5
7	20(15)	27.5	35	27.5
8	0	0	0	0
9	0	0	0	0

Table 6.4: Experimental results for numbers of prey eaten. The expected values are calculated on the assumption of the null hypothesis. * denotes total number of 'cemented' eaten, numbers in brackets are the number of these pulled free and eaten.

Figure 6.6 shows graphically the results of Experiments 10 and 11

Out of thirty one byssate bivalves consumed in Experiment 1, seventeen had been daubed with epoxy resin, thus demonstrating that the cementing agent *did not* inhibit predatory activity, perhaps by masking metabolite cues.

a)



b)

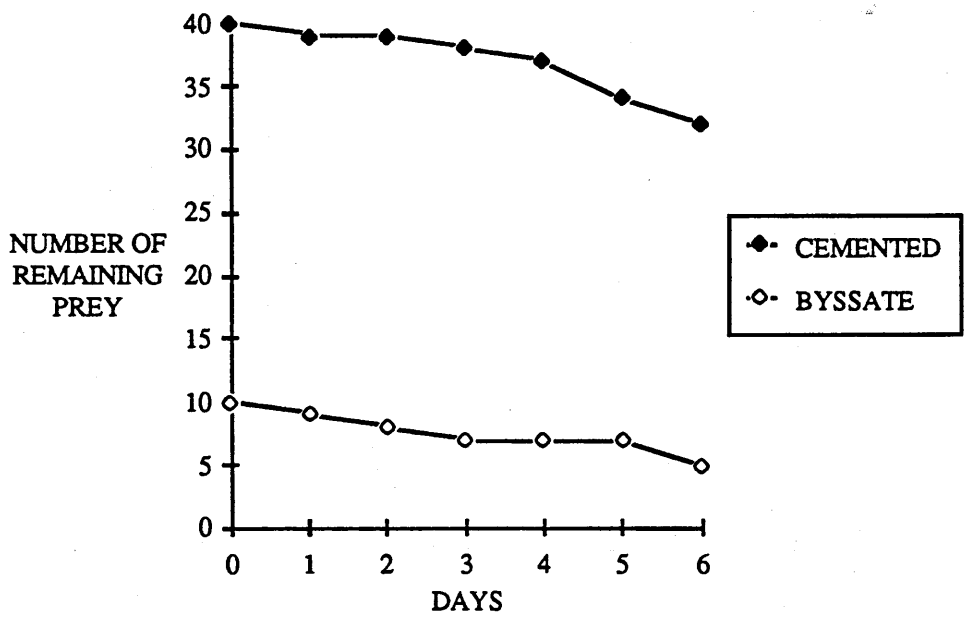


Figure 6.6: Results of non-replinishment experiments (a) experiment 10, and (b) experiment 11.

Failure of the gastropod experiments

Over a fourteen day period neither *Nucella* nor *Buccinum* consumed any prey. The failure of the *Buccinum* experiment may be attributed to poor predator choice on my part. Although Ansell (personal communication) and Hancock (1960) suggest that

whelks do take mussels, a more detailed study by Nielsen (1975) indicates that only sick *Mytilus* are taken. The failure of the *Nucella* experiment is more problematical. Dogwhelks *do* frequently feed on mussels (Hughes and Drewett, 1985 and Burrows and Hughes, 1989). The latter authors do suggest that foraging behaviour in *Nucella* is closely linked to the weather, the dogwhelks being more active in warmer periods. I am satisfied that the presence of epoxy resin in a tank does not inhibit feeding in dogwhelks, from tank observations at the OU. It therefore seems most likely that the weather experienced during the trials in November 1989 was not conducive to foraging.

6.3.3.3.4 Analyses of results and discussion

Table 6.4 clearly shows that the the actual results differed from those predicted by the null hypothesis; many more byssate individuals were taken. Two statistical methods were used to test this deviation from the predictions;, the one sample binomial test and the chi-squared one sample test. Formulae were taken from Siegel (1956), *Non parametric statistics for the behavioural sciences*. In order to reject the null hypothesis at a significance level of 5% values of z and $\chi 2$ needed to exceed 1.56 and 3.84, respectively. Rejection of the null hypothesis at the 1% level of significance is possible when z values are greater than 2.32 and $\chi 2$ exceeds 6.64.

For all analyses those bivalves pulled free and eaten were regarded as 'cemented' in addition to those which remained glued to the substratum. Although this probably overestimates the number of bivalves eaten in this category it provides a useful failsafe for the statistics and takes into account the observation of Feifarek (1987) that *Spondylus americanas* may be "broken away from the site of attachment." by its predators.

EXPERIMENT	z	P<5%	P<1%	$\chi 2$	P<5%	P<1%
1	3.3	+	+	12.1	+	+
2	1.8	+	-	4.2	+	-
3	6.18	+	+	39.3	+	+
4	5.2	+	+	27	+	+
5	3.26	+	+	7.5	+	+
6	1.9	+	-	4.5	+	-
7	1.8	+	-	4.1	+	-

Table 6.5 Statistical analysis of results, calculation of z from the binomial test and $\chi 2$ from the chi-squared one sample test. For method see Siegel (1956). Levels of significance at which the null hypothesis may be rejected are given. +=H_0 rejected and -=H_0 not rejected at the level cited.

In all cases the null hypothesis is rejected at 5% or less level of significance, see Table 6.5 Hence, we may confidently suggest that cemented prey are at significantly less risk from predators than are the byssate prey.

Discussion

Foraging experiments are notorious for producing erroneous conclusions. Manipulating parameters may cause the experimental conditions to be atypical of that found in nature, or it may be impossible to recognise and remove all extraneous parameters which are involved in prey choice. Thus it is possible to design an experiment to test one hypothesis, which in reality tests a multitude. Hence it was vital that the experiment described above was rigorously designed and carried out. I have complete confidence that the only parameter on which the prey choice was being made was that of prey attachment, and that the tank conditions were as 'normal' as possible, and that these results could be replicated by another experimenter. The amount of data presented here exceeds that given in many other foraging studies, e.g. Lake, Jones and Paul (1987) and Lawton (1989). Nearly 500 *Mytilus* were sacrificed in this experiment and all but experiment 6 were replicated.

Observations on the predatory behaviour (Experiment 3) suggested that although it was perfectly possible for the predators to eat the 'cemented' prey, it was more difficult to do so. This may be explained in terms of prey manipulation. Both asteroids and crabs require to manipulate their prey before ingestion (see Figures 6.7 and 6.8). When *Asterias* encounters a prey bivalve it rotates it until the postero-ventral valve margins are opposite its own oral region, and in assuming the classic humped feeding position the starfish pulls the mussel upright such that the commissure is perpendicular to the substratum. The crabs seize prey items in the master chela and rotate them, both to assess the size in the manner described by Elner and Hughes (1978) and to locate the weakest area for crushing. All of these movements are uninhibited by byssal attachment; the mussel may either rotate around its byssus, or some or all of the threads may be severed. Cementation, however, inhibits such movements, unless attached to a substratum of small enough size to be manipulated with the prey. In the experiments some of the predators used unorthodox methods to attack 'cemented' prey. For example several of the *Asterias* broke the valves of 'cemented' mussels, see Figure 6.9 (b). Hancock (1965) reports similar breakage of *Mytilus* by starfish in populations with large adductors, i.e. difficult to open. The usual result of *Carcinus* and *Cancer* feeding is to reduce the mussel shell into small fragments. However, some *Carcinus* took 'cemented' prey by neatly slicing through the ligament leaving both valves intact, see Figure 6.9 (c and d) . Cunningham (1983) indicates that if *Carcinus* is given a glut of suboptimal prey they are capable of learning to improve and modify their prey handling strategies. This may be a satisfactory explanation for the behaviour observed here.

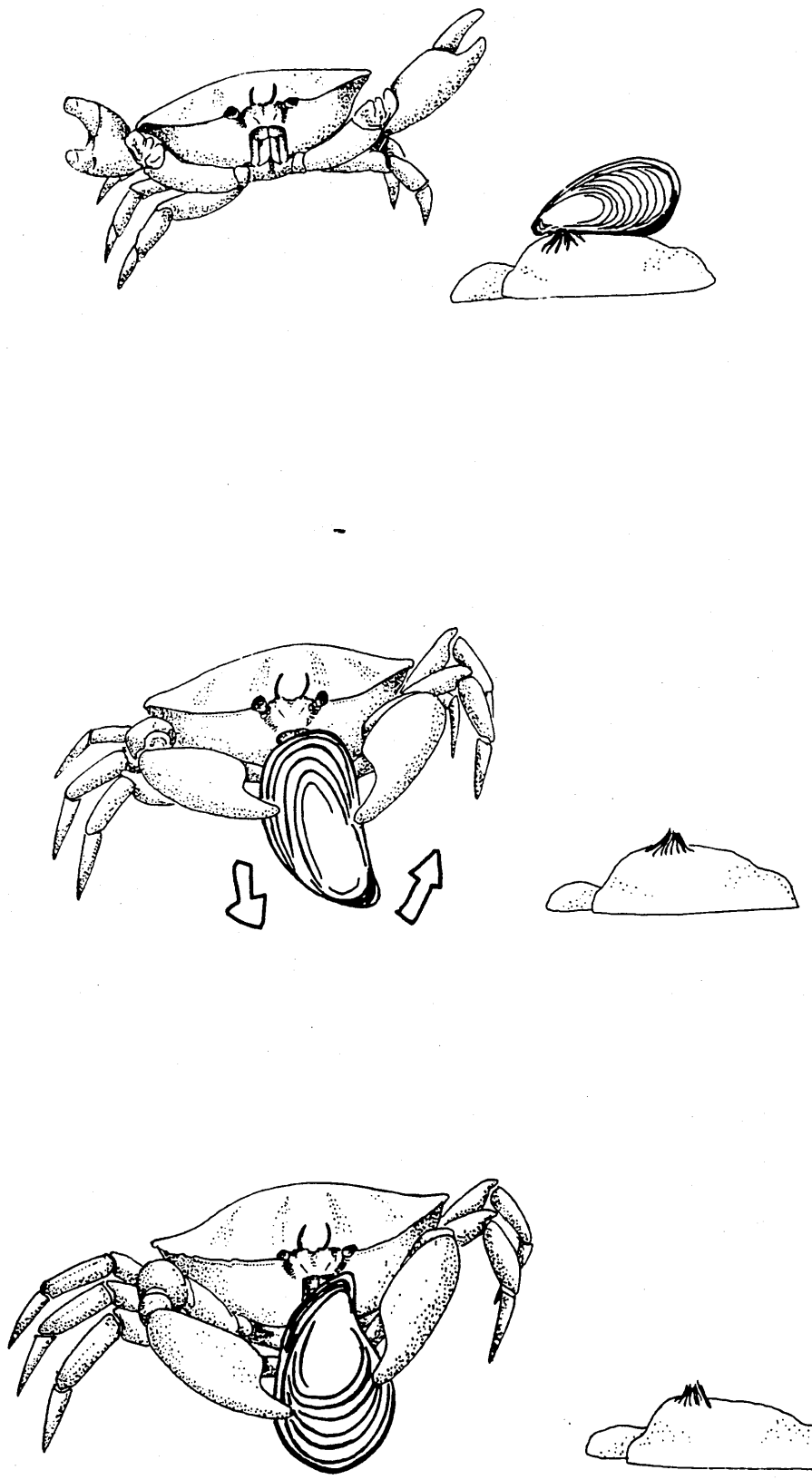


Figure 6.7: Illustration of *Carcinus* feeding on a byssate mussel showing the prey manipulation involved. Drawn by Camp.

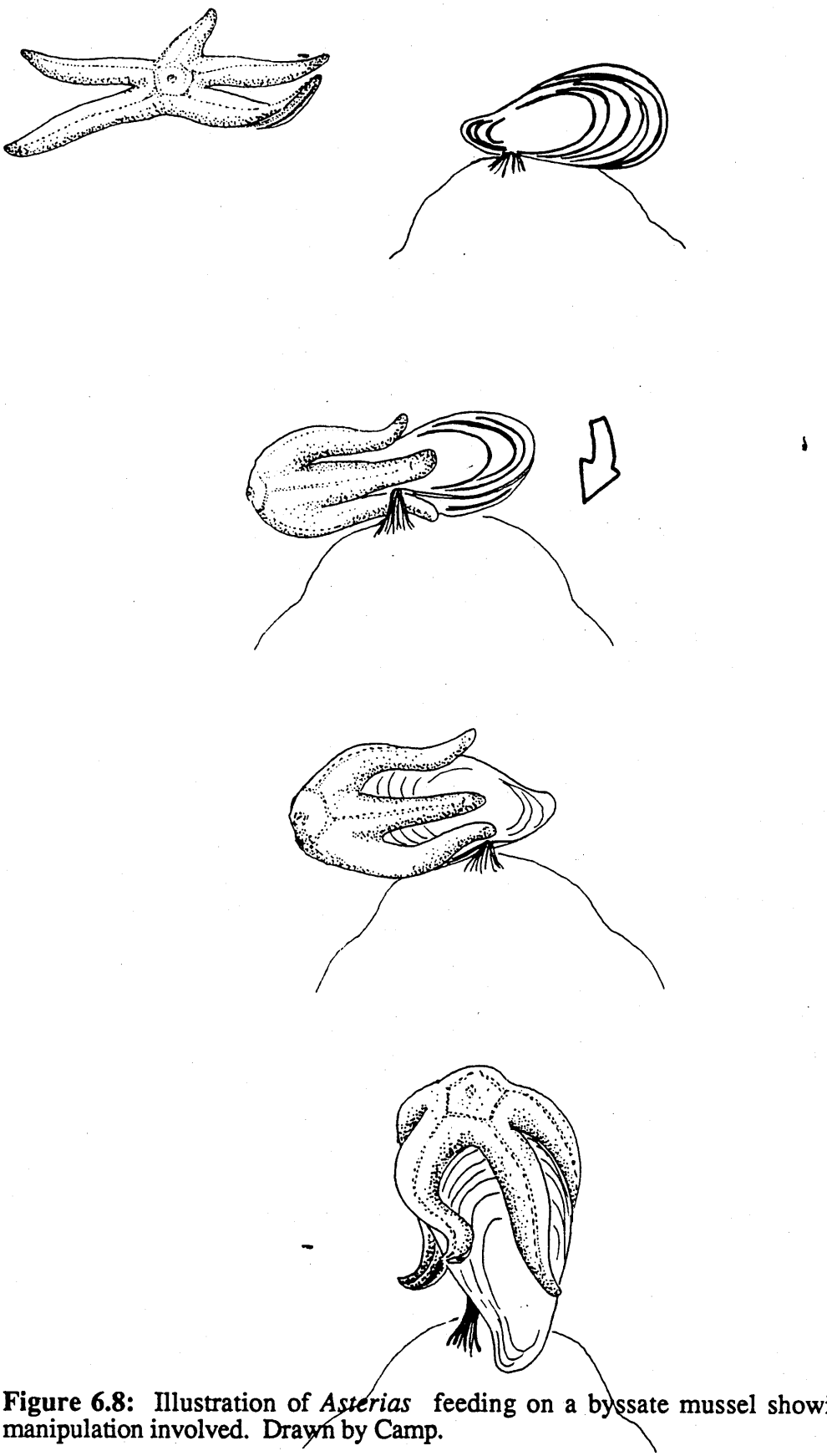


Figure 6.8: Illustration of *Asterias* feeding on a byssate mussel showing prey manipulation involved. Drawn by Camp.

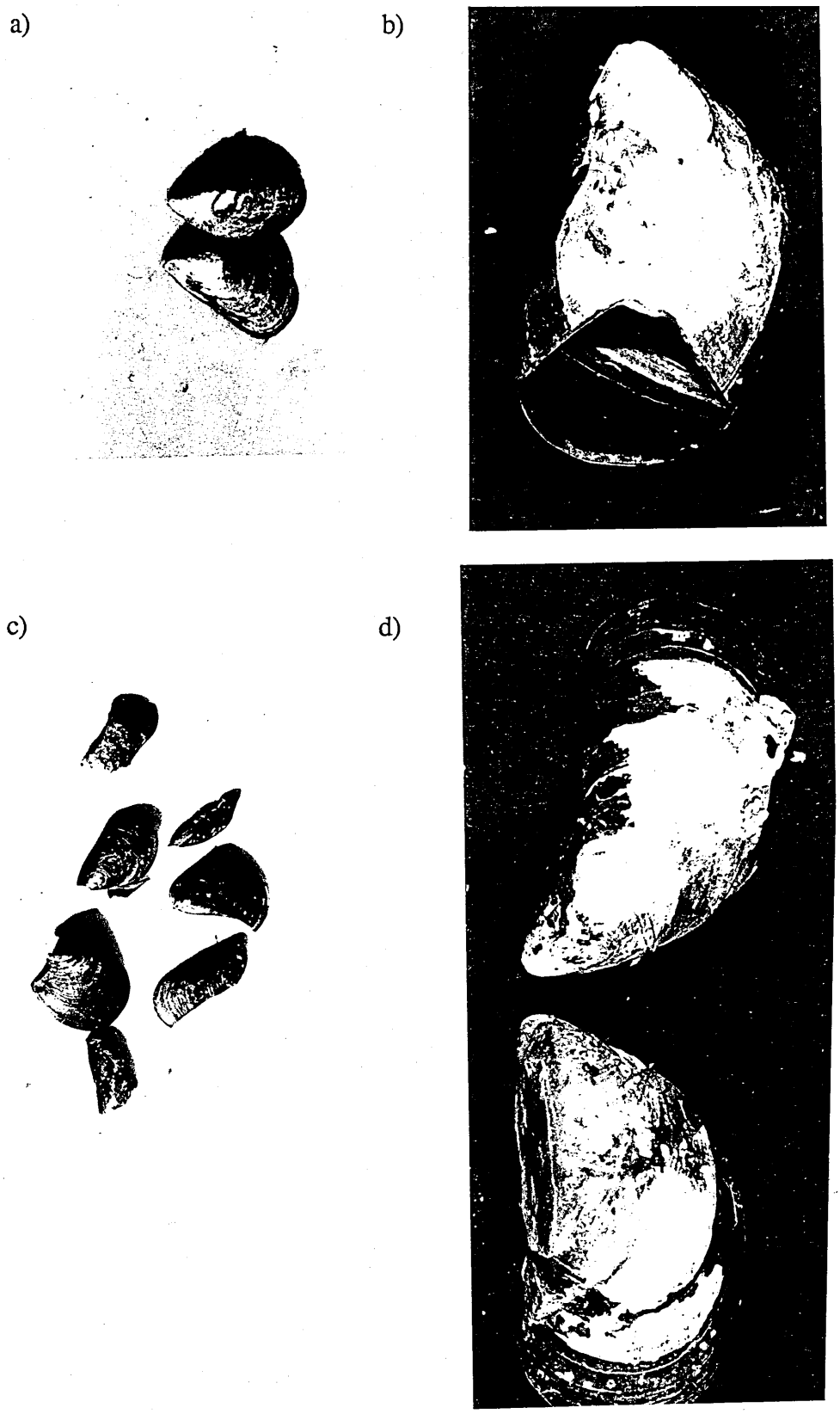


Figure 6.9: Characteristic predation damage on *Mytilus edulis* by; (a+b) *Asterias rubens,* showing (a) the more normal debris and (b) the broken valves produced in a minority of cases, (c) *Cancer pagurus* and *Carcinus maenas* and (d) *Carcinus maenas* (atypical debris).

Detailed observation of Experiment 3 every thirty minutes for two days revealed 76 attacks by *Asterias* (an attack is defined by the assumption of the humped feeding position), and of these 89% ended in failure. 55% of the attacks were on byssate prey, the remaining on the 'cemented'. This indicates that at the prey recognition stage of the attack there was no distinction made between the two prey types. However, of the 8 attacks taken to completion, only 1 was on a 'cemented' mussel. The time elapsed before discontinuation of a failed attack varied, averaging 1-1.5 hours for the 'cemented' and 3-3.5 hours for the byssate prey. Frequently the predator moved on for another attack, indicating that it had made a distinct prey choice rather than merely losing its appetite !

The valve height was determined for each of the 121 victims of experiment 3 giving mean values of 35mm for byssate and 32mm 'cemented' prey respectively. Statistical analysis by Student's t-test shows that there is no significant difference between the two.

It seems reasonable to interpret these results in the light of optimal foraging theory. The concept of Optimal Foraging was introduced to behavioural ecology in 1966 by MacArthur and Pianka (1966) and Emlen (1966). Since that year the premise has gained great credence and has been applied in a vast number of instances. In essence the theory states that predators are capable of evaluating prey quality and of making economic decisions in order to maximise their energy intake. The energy gained by the ingestion of a given prey item is reduced by the energy expended to locate, subjugate and ingest it. According to the theory predators will preferentially take prey which provide the highest net energy yield. Experimental work has confirmed that predators *do* optimise their diets. For example, Elner and Hughes (1978) show that *Carcinus maenas*, when confronted with a range of different mussel sizes will select from a very narrow size class; the actual prey taken agrees very closely with that predicted by the model, based on calorific measurements and assessment of handling time. This choice is made after considerable investigation of the potential prey. Larger

mussels, with a high energy yield, nevertheless require a large amount of manipulation, whilst smaller prey contain less meat for the effort spent. Other examples and a fuller account of the theory are given in Krebs and Davies (1981).

It would seem that the asteroid and crustacean predators used in this experiment were making such economic decisions based on exploratory assessment of the prey. Prey items in the tanks, of equivalent size are of equal calorific value, but the amount of time and energy required to access a 'cemented' prey is greater than that for a byssate prey. Therefore it is preferable in terms of optimising the energy intake for the predator to select the more easily manipulated prey attached by a flexible byssus than the more rigidly 'cemented' prey.

Since *Mytilus* was used as a prey species for both byssate and cemented categories, the calorific content of two equally sized individuals, which differ only in attachment, will be equal. Given that the 'cemented' prey are more difficult to manipulate and open than the byssate prey, the highest net energy yield will be gained by selecting the latter.

Various other authors have discovered that the crustaceans used here feed optimally, for example, Lawton (1983, 1989), Elner and Hughes (1978) and Cunningham (1983). I am unaware of any previous evidence of *Asterias* choosing a diet to maximise its energy intake.

Non replenishment Experiments 10 and 11 back up this interpretation, although there are insufficient data to be statistically valid. They suggest that even when the desired prey is only infrequently encountered they are still sought out.

6.3.3.4 Further evidence

The above experiments were conducted using non cementing bivalves. It is far easier to model a cemented bivalve with a byssate example than vice versa. The next step is obvious; it is necessary to consider the relative vulnerability of attached and nonattached cementing bivalves.

The oyster farmers provide a neat reverse of my experiment. As mentioned in Chapter 3 commercially grown oysters are either grown on small cultch or, more commonly, detached from collectors at an early stage. Seed *Crassostrea gigas* grown by the MAFF are separated from their substrates at less than twenty four hours after settlement (Sue Utting, personal communication). This separation appears to be standard practice all around the world (see Roughley, 1922; and Yonge, 1960), its advantages lying in the easy manipulation of the growing oyster by the farmer and the removal of the disfiguring morphologies produced by attachment to irregular substrates. But such ease of manipulation for the farmer is also enjoyed by the predators. Oyster beds are feeding ground for multitudes of predatory groups; gastropods, asteroids, crustaceans, fish, turbellarians and birds (Galtsoff, 1964), and the losses incurred are substantial (Galtsoff and Loosanoff, 1939). It is important to determine to what extent this is due to the loss of attachment. Mackenzie (1970) demonstrates that mud crabs rarely take attached oyster spat over 10mm high, whereas spat detached from the cultch are readily taken up to 25mm high. Krantz and Chamberlain (1978), working on the predation by *Callinectes sapidus* on cultchless spat note, "all that was required was that the blue crabs pick up and manipulate the oyster spats in their claws.... in this situation edges of the cultchless spat were accessible, in contrast to spat on an oyster cultch." Further evidence that predators require to manipulate oyster prey is given by Hickman (1972) discussing experiments on rock lobsters feeding on detached *Ostrea lutraria*. He states "..oyster *held vertically* between the front two pairs of walking legs while pieces of shell were broken off around the hinge by the mandibles. The position of the oyster is *reversed* to enable shell around the ventral margin to be broken off." (my italics).

Lunz (1947) does describe *Callinectes* feeding successfully on attached oysters, but these were attached to cardboard dipped in cement, and he clearly states that the crabs were able to tear away the cardboard to reach the prey. It would therefore seem apparent that by detaching oyster spat, ostreiculturists are increasing their vulnerability

to predation and many of the above authors suggest netting and other means to exclude predators.

However, Lau (1987) does report successful predation on attached *Ostrea sandvicensis* by the slipper lobster *Scyllarides squammosus*. He describes a wedging attack, unknown in other decapod crustacea, where the first and second pereiopod pairs are used to wedge open the valves as the third pair slice through the adductor and the remainder brace the bivalve. In this instance it would seem that the lobster is actually exploiting the rigidity of the oyster's cementation.

Evidence from other cementing bivalves is more anecdotal. Most diet determinations are carried out in tanks by offering a predator various food items, i.e. presenting them with detached specimens and are hence of little use here. Hartwick, Tulloch and MacDonald (1981) discovered that the cemented rock scallop *Hinnites multirugosus* comprised only 1% of the diet of *Octopus dolfleini* despite its common occurrence in or close to the octopod's den. Feifarek (1987) detached *Spondylus americanus* and transplanted them into shallow water, where they suffered a much higher predation rate. He attributed this to a higher vulnerability in shallow water, but I feel that it could just as well be interpreted as due to decreased predation resistance due to detachment.

Muntz, Ebling and Kitching (1965) offered the crabs *Carcinus maenas* and *Portunus puber* the choice of *Chlamys varia* (some byssally attached and others free) and attached *Anomia ephippium*, observing that only the former were eaten. Further experiments giving starved lobsters a tank of *Anomia* led to no predation. It is unclear whether we should interpret this as due to the lack of manipulability of anomiids or perhaps a lack of palatibility.

Interestingly Griffiths and Siederer (1980) found that the rock lobster, *Jasus lalandii*, takes *Choromytilus* preferentially to *Aulacomya* apparently because, although both are byssate, the former is more easily detached.

6.3.3.4 Application of the experimental work

The above experiment demonstrates a feeding preference of modern asteroids and decapods for byssate rather than cemented prey. I believe that this experimental work may provide an explanation for the sudden appearance of cementation in early Mesozoic bivalve taxa. It is intuitively obvious that, as far as predation pressure is concerned, any bivalve which evolves the cemented habit will be at a selective advantage over similar byssate friends. I argue that the onset of the MMR was causally related to the assumption of the cemented habit.

Cementation and gastropod predation?

Feeding trials involving gastropods failed to produce any data. It would seem very unlikely that the cemented bivalves would show any advantage in avoiding drilling over byssate forms; thus one would expect the null hypothesis not to be rejected. Gastropods do not manipulate their prey to any marked degree and it is quite possible that the rigid attachment provided by cementation may assist the predator. A specimen of *Nucella lapillus* held in the aquaria at the OU was observed twice to fall off a *Mytilus edulis* on which it was trying to drill. The prey, byssally fixed to the vertical tank walls, twisted around its byssal apparatus under the weight of the predator. Skelton, Crame, Morris and Harper (1990) note that the radiation of the drilling muricids and naticids in the Albian was actually accompanied by a reduction in the relative proportion of cemented bivalve taxa. We postulated that the cemented bivalves may have evolved other defensive adaptations in response to the drillers, such as the development of spines, chambered shells and the inclusion of chalky and conchiolin layers within the shell. The latter adaptations may be particularly relevant. Carriker (1980) shows that naticids drill with the aid of an acidic secretion. Taylor (in press) shows that naticid drill holes in modern *Saccostrea* frequently terminate at conchiolin layers, from which we may infer that the the acidic secretions are unable to penetrate the organic sheets. Currently work is underway to establish whether it is possible to trace these conchiolin sheets in fossil oysters, and if so, to determine their first appearance and their relationship to gastropod drill holes.

Galtsoff (1964) regards gastropods, for example the oyster drills *Urosalpinx* and *Eupleura* , as the "deadliest enemies of oysters". Clearly gastropods are able to penetrate the shells of modern cementing bivalves and have done so in the past e.g. Tertiary specimens of *Dimyodon deshayesiana* NHP 69922 and *Dimya dissimilis* NHP L4888.

6.3.3.6 A plausible explanation?

Skelton et al (1990) explore the adaptive divergence of post-Palaeozoic bivalves. We showed how the decline in byssate taxa at the end of the Palaeozoic resulted in the expansion of other adaptive zones, for example the swimming, cemented, and boring habits, and that these were not merely a result of the diversification of Palaeozoic exponents of those habits but were acquired as new innovations in many clades. We regard the MMR to be of crucial importance in this radiation. Other authors have also invoked the increasing predation pressure as favouring the acquisition of various life habits, e.g Stanley (1977) for the rise of the siphonate burrowers and Carter (1978) for that of the boring bivalves. Feifarek (1987) and Vance (1978) also attribute the growth of spines as having a defensive function in epifaunal bivalves either in a primary role or as settlement sites for camouflaging epibionts.

The MMR has also shown its effects in the evolution of other phyla. Palmer (1982) recognised that, compared with Palaeozoic examples, Mesozoic hardground communities contain more skeletonised and infaunal taxa. He attributed this to the radiation of predators at this time, but also acknowleged the consequent increase in scour resistance. Aronson (1989), testing the hypothesis that the decline in the number of ophiuroid beds in the Phanerozoic was due to increased predation pressure rather than changing taphonomic bias, concluded in favour of the predation hypothesis. Most recently Donovan and Gale (1990) have published on the role of the neoasteroids in the decline of the articulate brachiopods. They recognise the impact of the evolution of the extraoral feeding mode in the neoasteroids at the start of the

Mesozoic would have had on epifaunal communities, in particular on the brachiopods with their poor capacity for defense.

Although Signor and Brett (1984) document a mid Palaeozoic precursor for the MMR, none of the predatory groups they describe as evolving in the Middle Devonian is thought to have utilised manipulatory methods to feed, and therefore would not have favoured a rise of the cemented habit.

Criticism

Fortey (personal communication) attacks the very concept of the MMR as an important selection pressure; he regards such hypotheses as untestable. I would choose to defend the use of it in my work on the following grounds:

-The experimental work shows that modern molluscivores do prefer byssate to cemented prey. This is demonstrable with statistically significant data and not a mere supposition.

-The experimental work was designed to be realistic. Chapter 4 demonstates that most if not all cemented bivalves have byssate origins. Hence the experiment does test the advantages for byssate bivalves becoming cemented.

-For economic reasons modern molluscivores have been intensively studied. Aside from gastropods, the principle molluscan predators are crustaceans and asteroids, both participants in the early MMR. For example, Galtsoff and Loosanoff (1939) describe 6,987,650 asteroids feeding from 1,500 acres of oyster grounds in Narragansett Bay, USA, in 1931. The key to their voracity is the extra oral feeding mode which Gale (1987) clearly establishes appeared in the Triassic. The use in the experiments of these predators was therefore relevant to testing the palaeontological hypothesis.

6.4 FUTURE WORK

Predation is a key ecological interaction. The penalties of being eaten are high; as far as passing on a large number of genes into the next generation is concerned, being eaten is one of the worst possible strategies. As Dawkins and Krebs (1978) state in their reasoning that prey are always ahead in the evolutionary arms race " A fox may reproduce after losing a race against a rabbit. No rabbit has ever reproduced after losing a race against a fox.". One of the problems with assessing the impact of predation on evolution is that actual fossil evidence is hard to come by. The argument would be strengthened if we could assess the relative number of successful and unsuccessful attacks on early Mesozoic byssate and cementing bivalves. However, unlike the drilling gastropods, the major predator groups in which we are interested produce no diagnostic debris and as yet we have no way of distinguishing it in the fossil record from that produced by abiotic taphonomic processes. The vast amount of material necessary for such a study to be meaningful would need to be collected specifically for that purpose. Museum material cannot give a satisfactory database because of the collecting bias towards whole, pristine specimens rather than those mangled beyond recognition by predators. Current records of fossil predation on molluscs, in particular bivalves, are mainly anecdotal, e.g. Kauffman's (1972) report of the holotype of *Inoceramus tenuis* having been bitten, allegedly by *Ptychodus*. Although interesting enough, such isolated observations fail to address any of the really important questions involved with predation, as was recognised by Speden (1971) and Carter (1968) in their attempts to place fossil examples of predation on bivalves into a more ecological context. The notable exception to these criticisms are the accounts of predation on and by gastropods by Vermeij and his coauthors (see Vermeij 1987 and his references therein) and Kelley (1989); both these authors made important contributions to understanding the evolutionary adaptations in response to predation pressure. However, given that the shellfisheries literature on modern molluscivores is so great, the fossil record of bivalves is good and the bivalve construction so susceptible to lethal injury (Vermeij 1983), there is much scope for

future investigation of predation in the fossil record which may be able to provide the fossil evidence for the work described here. In relation to this problem I intend to undertake the following work;

1] Cementation has produced a group of bivalves which are literally sitting targets for gastropod predation. It will be necessary to investigate defensive adaptations which arose in response to this threat and in particular to assess the role of conchiolin sheets in the shell structure of the oysters in relation to gastropod predation.

2] Chapter 3 has established that the cemented condition in the Chamacea produces only a weak bond to the substratum. How does this attachment rate as an antipredatory device?

6.5 CONCLUSIONS

1] There are a number of advantages to the primitive byssate habit not shared with the derived cemented attachment. These chiefly result from the non permanence and flexibility of the threads.

2] The major cemented bivalve clades evolved early in the Mesozoic. This is not coincident with any notable abiotic change in the environment but does closely tie in with the Mesozoic Marine Revolution (MMR).

3] Experimental evidence suggests that modern molluscivores prefer byssate to cemented prey. This is interpreted as optimal foraging; the cemented bivalves are more difficult to handle thus resulting in a lower net energy intake.

4] I am suggesting from the experimental evidence that the rise of cementation in the bivalves is causally linked to the MMR. The need to avoid predation is paramount; cementation to a hard substratum is a means for some epifaunal bivalves to achieve this.

5] This study indicates the potential of the use of the behavioural studies in tackling palaeobiological problems.

CHAPTER 7

CONCLUSIONS AND IMPLICATIONS

7.1 INTRODUCTION

The aim of this final chapter is to take a broader view of the information given in this thesis. Four major sections are included:

(i) A synthesis of conclusions on the evolution of the cemented habit in specific bivalve clades, with a summary of outstanding problems.

(ii) An identification of the constraints which have prevented the habit from becoming more widespread.

(iii) The implications of this research for our understanding of the mechanisms of bioimmuration - an important phenomenon associated with cementing bivalves.

(iv) The implications for understanding cementation in other encrusting taxa and suggestions for further work.

7.2 THE EVOLUTION OF THE CEMENTED HABIT IN THE BIVALVES

7.2.1 Conclusions from thesis

The bulk of this thesis has striven to explain the multiple evolution of cementation in the bivalves. It has been demonstrated that cemented attachment may be achieved by relatively simple modifications of the normal shell secreting processes. Such modifications are easily attained; indeed many bivalves are preadapted for the habit by virtue of other adaptations. For example, selection pressures favouring the assumption of a pleurothetic orientation, thinning of the periostracum (e.g. for decreased water resistance), or increased extensibility of the mantle margins (e.g. to increase sensory perception) are preadaptive to the evolution of cementation. The

Pectinidae appear to be particularly well preadapted in these respects, and cementation has independently evolved within that family at least four times since the Jurassic. Although most of these preadaptations are modifications of soft parts, I have explored methods to infer information about the evolution of these characters from palaeontological material.

Cementation inhibits a predator's ability to manipulate its prey and hence enhances the bivalve's survival. I have proposed that the increased predation of the MMR played an important role in the evolution of the cemented habit.

7.2.2 Outstanding problems

These novel studies have established the mechanism of cementation and suggested the morphological preadaptations and the environmental conditions which are likely to have facilitated the evolution of this mechanism. It should now be possible to make detailed studies of the evolution of the habit within specific clades. The current work has volunteered very little information about the ancestry of specific cemented clades, and only *Chlamys pusio* has been 'caught in the act' of evolving the habit. Questions surrounding the evolution of the habit within important groups, such as the oysters, remain unanswered.

Detailed palaeoecological studies are now required, particularly in rocks of early Mesozoic age, to follow the appearances of the habit in each clade. The work described herein should provide a useful framework of characters to investigate and the general characteristics which putative ancestors should possess. Suggestions have been made about the possible role of heterochrony in the evolution of the habit and also a possible relationship between cement mineralogy and ocean chemistry. These hypotheses may be confirmed or refuted by further study of palaeontological material.

7.3 CONSTRAINTS

We are entitled to reverse the original enquiry. If cementation is so advantageous and so easily acquired, why is the habit not more widely spread? What are the constraints which prevent other bivalves from cementing?

Nicol (1978) asked this very question and provided four possible answers:

(i) Cementation precludes the possibility of deposit feeding, thereby debarring all those bivalve taxa which feed in this manner.

(ii) Cemented bivalves are latitudinally restricted to warmer waters.

(iii) Cemented bivalves require wide spacing of inhalant and exhalant currents.

(iv) There is no selective advantage in cementation.

Of these Nicol regards the fourth, the lack of selective advantage, as paramount. However, Chapter 6 has demonstrated this view to be untenable. His first explanation, although undoubtedly true, does not explain why certain byssate epifaunal suspension feeders do not cement. Likewise the problem of separating the inhalant and exhalant currents, the third constraint, is not faced by cementing bivalves alone, but is also relevant to byssate bivalves.

The only really plausible explanation offered by Nicol is the limitation of cementing bivalves to warmer waters. This limitation has been explained in terms of the cementation process in Section 4.5.2. Even though warm seawater temperatures do, I believe, facilitate the formation of the cement, it is not the only limiting factor. We must search for other constraining factors.

The question, in fairness, should be directed only at the epifaunal bivalves associated with hard substrata, in particularly those attached by a byssus. The course of bivalve evolution has not been unidirectional; Chapter 1 outlines the broad adaptive repertoire of the class which has allowed them to exploit so many niches. Certain of these adaptive courses are not compatible with cementation. For example, those bivalves which live on or in soft substrates are seldom in a position where cementation would be possible.

7.3.1 Evolutionary constraints

The question of evolutionary constraints has been dealt with by Seilacher (1970) in his proposition that organic structure should be examined in terms of three interacting factors:

(i) Historical-phylogenetic factors relating to an organism's bauplan.

(ii) Constructional factors imposed by the mode of growth and the limits of the materials available to the organism.

(iii) Functional factors relating to aspects of functional morphology which are directly influenced through natural selection.

In a broader sense constraints may be viewed as intrinsic (those imposed by the organism itself, i.e. Seilacher's formulation) and extrinsic (those relating to ecological pressures and environmental factors). It is, perhaps, the relative roles of intrinsic and extrinsic constraints in the course of evolution which is most interesting. Skelton (in press) points out that adaptive radiations involve both extrinsic and intrinsic factors, but that one will act as the cue for adaptive change in any instance whilst the other is the enabling circumstance. When considering constraints in adaptive radiations we may turn Skelton's formulation around. In the case of epifaunal bivalves which do not cement we must consider which is absent: the apparent extrinsic cue of increased predation pressure or the intrinsic morphological requirements which preadapt the organism for the habit?

Thomas (1978a,b) has made a specific investigation of constraints in bivalve evolution, with reference to the Arcacea. Thomas considers the evolutionary conservatism of the arcs as a consequence of constructional constraints imposed by a weak ligament, strong taxodont dentition and their inability to form siphons. He sees the repetition of a limited number of evolutionary innovations within the superfamily as "...as much a function of their limited range of shell growth as it is of common adaptation to a single environment." (Thomas 1978(b), p335).

7.3.2 The mussels: could they cement?

Figure 7.1: *Mytilus edulis* living intertidally in Dunstaffnage Bay (Oban) outside the marine station.

Throughout this study I have used the edible mussel, *Mytilus edulis* (see Figure 7.1) as a foil against the cementing bivalves. Not only is this species the most conveniently obtainable non-cementing epifaunal bivalve, virtually ubiquitous on these shores as well as being available on fishmongers slabs in the inland resort of Milton Keynes, but it also epitomises those epibyssate bivalves which appear to have been prevented from cementing. Therefore the mussel is an ideal subject of investigations to consider the constraints which inhibit cementation.

Care must be taken that circular arguments be avoided. It is to be noted that the conclusions relating to the differences between cementing and non-cementing bivalves made in the previous chapters have not been made as a result of a straight comparison between *Mytilus* and various cementing bivalves. Instead comparison has been made with a whole range of non-cementers.

7.3.2.1 The Mytiloids

Mytilus, of the superfamily Mytilacea, belongs to the ancient Isofilibranch order Mytiloida (Waller, 1978). Although La Rocque and Newell in the *Treatise* (Moore, 1969) give the range of that order as Devonian to Recent, there is evidence that many 'mytiloid' characters can be found in earlier Palaeozoic bivalves. Pojeta (1971) suggests that the Ordovician Modiomorphidae are greatly similar and likely to have been ancestral to the Mytilacea, a view reiterated in Pojeta and Palmer (1976). Certainly these early Palaeozoic bivalves seem to have had life habits like those of Recent mussels. If we accept this we are presented with a group of mytiliform bivalves with origins in the early Palaeozoic. Skelton et al. (1990) Figure 1 shows a plot of the number of families present in each of the post-Palaeozoic bivalve orders over geological time. From this it would appear that the mytiloids have enjoyed a persistent, if modest, taxonomic diversity since the early Mesozoic. Examination of their life habits reveals that the vast majority are byssate, either endobyssate, e.g. *Modiolus*, living attached semi-infaunally in soft sediments, or epibyssate, e.g. *Mytilus*, attached to firm substrates. A small number have also become adapted for boring into hard substrata, for example the Ordovician genus *Corallidomus* (Pojeta and Palmer, 1976) and the Mesozoic to Recent lithophagids (see Yonge, 1955), but even in these forms byssate attachment is maintained. Despite their long evolutionary history of association with hard substrata the mytiloids have never cemented.

Mussels form an important component of the diet of many marine predators. Chapter 6 has demonstrated that considerable advantage accrues to the artificially cemented mussel in the evasion of predation. What has prevented the group adopting, naturally,

this important anti-predatory life habit? The mytiloids occupy the same broad ecospace as many of the early cementing bivalves, i.e. attachment to hard substrates in shallow water environments, and would have experienced the same gross changes in seawater chemistry and temperature. There is, therefore, little suggestion that the constraints which prevented them from cementing were extrinsic. Hence it is the possible intrinsic constraints which must be explored.

7.3.2.2 Life orientation.

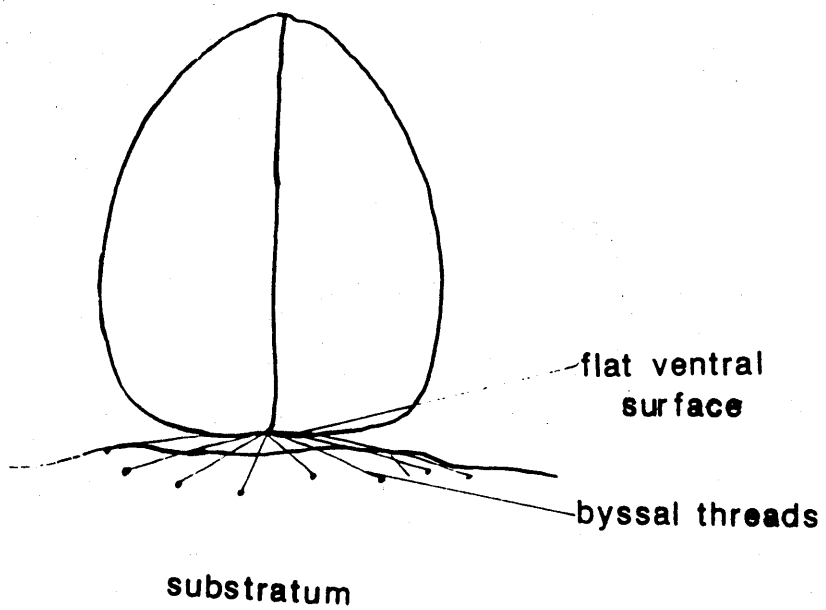


Figure 7.2: Cross section through an epibyssate mussel.

Section 4.3.1 stresses the requirement for cementing bivalves to adopt a position so that the mantle margins are closely adpressed to the substratum in order to allow shell/substratum overgrowth to occur. All mytiloids are orthothetic which does certainly limit mantle substratum contact. But as stated previously, although true in the majority of cases, not all cementing bivalves derive from pleurothetic stocks.

In any case the epibyssate mytiloids *do* present part of their valve secreting mantle edges close to the substratum. Epibyssate mytiloids are characterised by a flat ventral face to the valves around the emergent byssus which allows the animal to fit snugly against the attachment surface (see Figure 7.2) when pulled down by the action of the

pedal retractor muscles. This feature of the epibyssate mytilaceans as compared to the endobyssate members of the superfamily is discussed by Stanley (1972)

Hence, it is, I believe, not the the positioning of the mantle margins relative to the potential attachment surface in itself which prevents the mussels from cementing.

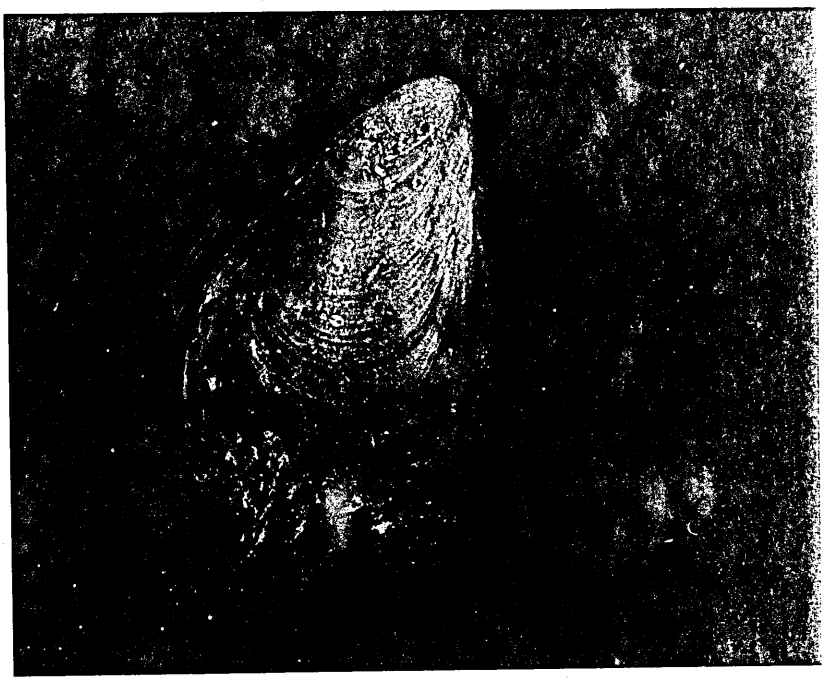
7.3.2.3. Capacity for valve distortion

Section 4.4.2 discusses the requirement for cementing bivalves to be able to construct 'lower' valves which follow substratal topography and, following Waller (1990), links this ability with reduced mantle rigidity. The latter may be inferred from the degree of distortion on both valves.

Examination of large numbers of Mytilacea in the collections of the NHZ has revealed that they have a very poor capacity for valve distortion. Such distortion that is observed appears to be unrelated to substratal topography. Figure 7.3 illustrates the right valves of two specimens of *Mytilus edulis* collected from Dunstaffnage Bay, Oban. Individual (a) was collected subtidally from the fish rafts in the bay, whilst (b) dwelt in the intertidal zone; both are characteristic of the clumps from which they were extracted.

The subtidal specimens are thin shelled (<0.5mm), very smooth shelled and in possession of an intact periostracum. By contrast the intertidal specimens are thicker shelled (>1mm), slightly distorted and with an incomplete periostracum. I believe these morphological differences may be attributed to their relative exposure to seawater. The continual immersion experienced by the subtidal mussels means, in theory, that the individuals can enjoy continuous feeding and valve growth. This leads to rapid valve accretion without the major disruptions liable to cause discontinuities which disfigure the valve. The intertidal mussels, however, are periodically deprived of seawater during which time they are deprived of the opportunity to grow and are subject to the rigours of desiccation and fluctuating temperatures. The stress of life in

A



B

Figure 7.3: *Mytilus edulis* collected from Dunstaffnage Bay (Oban) (a) subtidally attached to fish rafts, valve height = 51mm, and (b) intertidally, valve height 62mm.

the intertidal zone results in much slower growing mussels, gnarled by their start-stop mode of growth. The variation in growth rate may be inferred by the relative degree of epibiont cover. The 'fast' growing subtidal mussels lack such colonisation whilst the 'slow' growing intertidal individuals bear at least two generations of barnacles.

Other valve distortions I have observed in living mytilids are interpreted as resulting from marginal valve damage and repair, probably associated with failed predation attempts.

Apart from shell torsion in semi-infaunal species, reported by Savazzi (1984), there is no evidence that living mytilids are able to distort their valve growth to conform to substratal irregularities. This is probably due to an inability to lose mantle rigidity, but this has yet to be confirmed. I see this as a significant constraint preventing the mytiloids from cementing.

7.3.2.4. The periostracum

Recent Mytilacea are characterised by exceedingly thick periostraca. Of seventeen members of the superfamily from which estimates of periostracal thickness were made (see Figure 7.4) a minimum value was obtained for *Modiolus tulipa* (22μm) and a maximum for *Stavelia torta* (360μm). For over half of the species considered values fell into the range 50-80μm. It would seem that the periostracum of Recent Mytilacea is universally thick, regardless of life habit, whether epi- or endobyssate or boring.

Using the arguments given in Section 3.3.1.1, an infinitely flexible periostracum, of say 70μm, can only negotiate topographic valleys in the substratum of >140μm. But in reality periostracal sheets are not infinitely flexible, and the precision with which the sheet may follow irregularities is yet poorer. This failure to follow the configuration of the attachment surface is another significant bar to cementation.

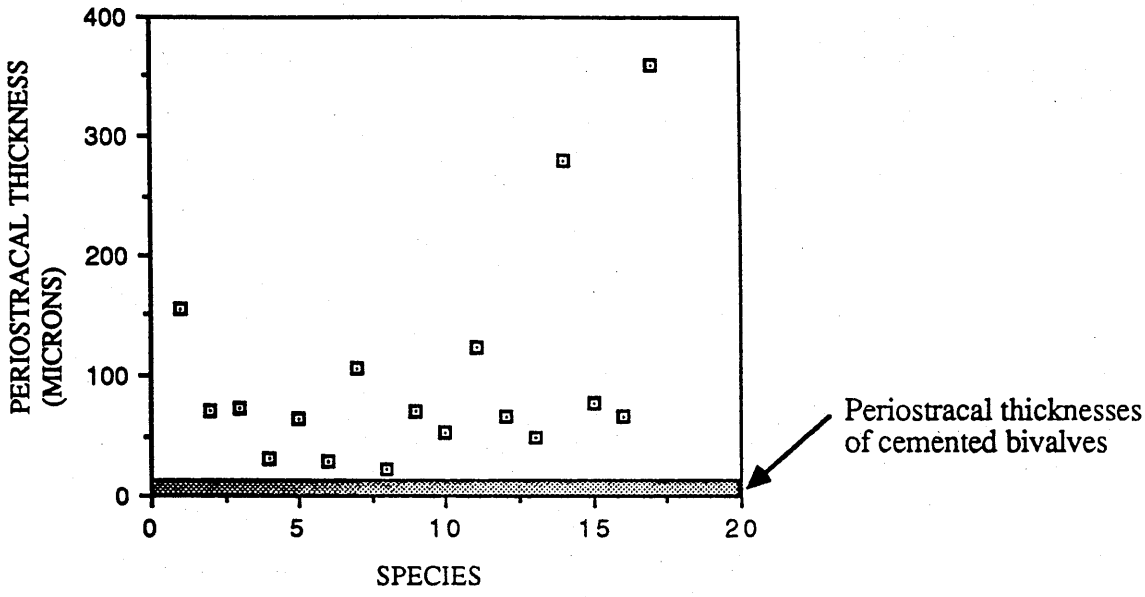


Figure 7.4: Periostracal thicknesses measured for Recent Mytilacea, data derived from Table 3.2 and plotted in alphabetical order. The stippled area represents the periostracal thickness values which have been obtained for cementing bivalves. It must be stressed that the size of this envelope is greatly increased by the thicker periostraca of the pandoracean cementers and that in the vast majority of cementing bivalves values of less than 1μm were recorded.

Clark (1976) regards the grossly thickened periostraca of the mytilids as just as derived as the extreme thinness of the ostreid periostracum. With no clear idea from palaeontological material as to the evolution of periostracal thickness over geological time (see Section 4.4.1) it is not possible to comment on this. The only thickness data known to me, derived from fossil mytiloids, is for the putative periostracum of the Jurassic *Praemytilus strathairdensis* measured at 5-15μm by Hudson (1968). This value is lower that those recorded for modern mytilids but the significance of this is questionable. The matter awaits the development of a reliable method to infer periostracal thickness from fossil material.

The periostracum of Mytilus edulis

The results of my investigations of the periostracum of *Mytilus edulis* are comparable to those published by Dunachie (1963). Intact sheets stripped from the outside of valves are shown to be thick, averaging 66μm, thickening towards the ligament and only moderately flexible. Many fractured sections viewed by SEM display a tri-layered structure, with two outer 'solid' layers flanking a vacuolated middle layer.

Where damage has been sustained to the outermost covering, details of these vacuoles are apparent (see Figure 7.5).

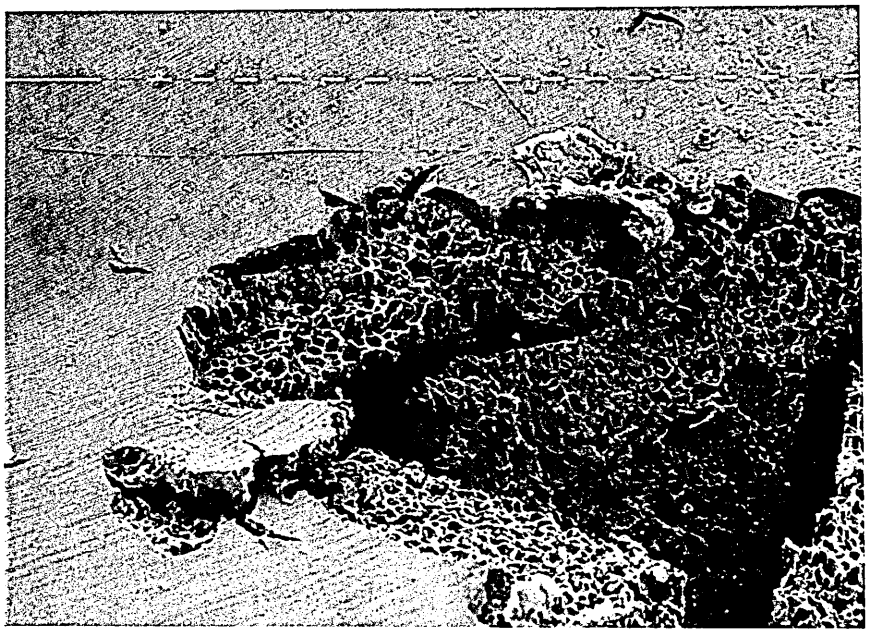


Figure 7.5: Damage to the outer surface of the periostracum of *Mytilus edulis* revealing central vacuolated layer. Critical Point Dried preparation, Stub EMH0130, small scale bar = 10μm.

Contrary to Dunachie's observations I have found that this central layer is not continuous over the entire valve, but has a rather patchy distribution. In the future it will be instructive to determine whether these patches are randomly placed or whether their distribution is constant between individuals. Such a study may also provide information as to the function of the vacuoles. Four possible functions are suggested below:

(i) The inclusion of a vacuolated layer may enable the mussel to construct a thick periostracum without wasteful manufacture of material.

(ii) Tevesz and Carter (1980) argue that these vacuoles are fluid filled, preventing desiccation during subaerial exposure, leading to cracking of the periostracum.

(iii) Skelton (personal communication) suggests that the vacuoles may inhibit the rasping activity of predatory gastropods.

(iv) Sponginess of the periostracum, conferred by the vacuoles, allows compression, enhancing the sealing of the valves during adduction - a considerable benefit in evading predation and for intertidal individuals prone to desiccation. Clark (1976) suggests a similar function in proposing that the spongy periostracum along the ventral valve margins can effectively seal the valves despite the presence of bulky byssal threads projecting between the valves.

Whatever their function, the presence of vacuoles in the periostracum is not universal within the Mytilacea. Of those species studied similar features have only been discovered in the green lipped mussel, *Perna viridis*.

There is no indication that the mytiloid periostracum has any mechanism for the transport of extrapallial fluid, although it is to be noted that the same is true for taxa, e.g. ostreids, where the process does undoubtedly occur. However, the dense nature of mytiloid periostraca contrasts with the gossamer appearance of the periostraca of cementing bivalves and such leakage is hard to envisage. Yet a mechanism for periostracal permeability does potentially exist in those species with vacuolated middle layers, if periostracum formation could be modified for the omission of the outer non-porous layers.

7.3.2.5 Mantle extensibility

Section 4.4.2.2 concludes that the cementing bivalves are characterised by highly extensible mantle margins and that this may be quantified by measurement of the dorsal inset of the pallial line (IR). IR data are recorded in Appendix 3, including values for 25 species (10 genera) of Recent Mytilacea. These values are almost universally low, indicating pallial line positioning close to the valve margins. Figure 7.6 plots the mean IR values for each species, along with their standard deviation (σ_{n-1}).

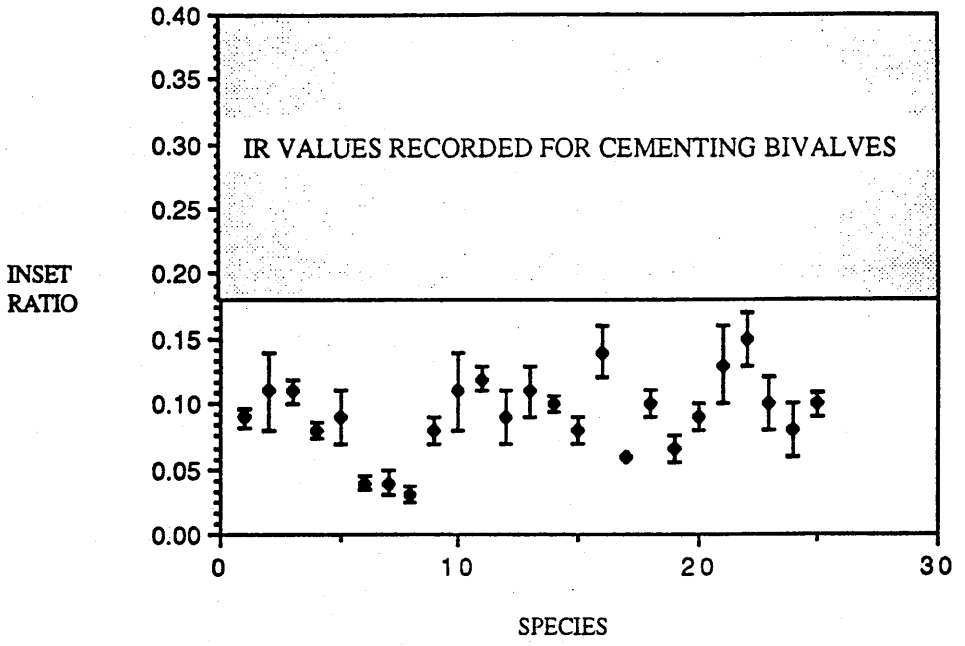


Figure 7.6: IR values and standard deviations for Recent Mytilacea, data from Appendix 3 plotted in alphabetical order. Stippled area represents IR values, also from Appendix 3, obtained from cementing bivalves.

The stippled area plots the range of IR values recorded for all individuals of cementing bivalves measured in this study. Clearly these two data sets are mutually exclusive.

The relationship between mantle extensibility and the ability of bivalves to manufacture spines and co-marginal flanges has been discussed in Section 4.4.3. No mytilids examined, either living or fossil, have been observed to possess valve outgrowths. This fact, together with the low IR values and tank observations of the behaviour of *Mytilus edulis*, suggests to me that the mussels lack the ability to extend the extrapallial cavity beyond the valve margins.

7.3.2.6 Summary of inferred constraints

From the study of the above it would seem that the epifaunal mussels are unable to cement because they lack the fundamental morphological requirements for the cementation process. A thick, inflexible and probably non-porous periostracum prevents extrapallial fluid leakage, whilst mantle lobes have a poor capacity to mimic substratal irregularities or even to extend and lay the periostracum directly on to the substratum. Cementation, therefore, is not a means by which this group can evade

predation. Nevertheless the living mytiloids enjoy successful colonization of hard substrates, as evidenced by *Mytilus* beds in temperate latitudes. There are significant advantages to strong byssate attachment, as reviewed in Section 6.2, chiefly centered upon the flexibility of attachment and its lack of permanence. Additionally the mussels have adapted to face the menace of predation by other means listed below

- The formation of densely packed gregarious clumps, tightly fixed to both substratum and each other, which prevents easy extraction of individuals and inhibits prey manipulation.
- The novel use of byssal threads to imprison predators (Petraitis, 1987).
- Mussels can also live in high energy environments where predation pressure is low. They also commonly inhabit the intertidal zone, a difficult environment for many predators, e.g. asteroids.

7.3.3 Others

Another important group to consider in the light of constraints is the Superfamily Anomiacea. Although I accept the byssal attachment of the anomiids as a form of cementation, complying with the definition given in Section 1.1, it is unquestionably quite distinct. Cementation in this superfamily has been brought about by modification of the byssal apparatus rather than the mantle. With the possible exception of the pectinid *Hemipecten forbesianus*, I know of no analogues to the anomiid attachment.

Preliminary studies show that modern anomiids possess very thin periostraca and that *Monia squama* and *Eonomia timida* have the capability of constructing their right valves deceptively close to the substratum. However, the number of individuals available for my study has been few, as yet insufficient for drawing conclusions. Quite why the anomiids have employed this form of cementation rather than the mechanism which has convergently evolved in so many other forms, or whether there are any selective advantages to this mode are matters for further investigation.

7.4 A MECHANISM FOR BIOIMMURATION?

Soft bodied organisms, with an ordinarily poor preservation potential, may be preserved as natural moulds if they are overgrown by skeletonised encrusting organisms such as cementing bivalves and serpulids. This mode of preservation, known as bioimmuration, is reviewed by Taylor (1990a). Taylor recognises three categories of bioimmuration: (i) substratum bioimmuration, where the bioimmured victim is the actual substratum colonised by the bioimmurer, (ii) epibiont bioimmuration, where the bioimmured organism is a fellow epibiont, and (iii) bioclaustration, a term proposed by Palmer and Wilson (1988), where the bioimmured organism occupied a life position embedded within the body of the bioimmurer. Of these, the cementing bivalves are most readily capable of the former two categories, although it is conceivable that organisms trapped between the mantle and valve may be preserved by bioclaustration (J. Todd, personal communication).

The potential of studies of bioimmured organisms is great. Taylor (1990b) demonstrates this with a description of the soft bodied ctenostome bryozoan genus *Cardoarachnidium* from Jurassic bioimmurations. By consequence of their lack of calcified hardparts the fossil record of the ctenostomes is poor and their evolutionary relationships previously enigmatic. However, Taylor has used information from bioimmurations to propose that these primitive bryozoans are the stem group of the widespread and abundant cheilostome Bryozoa.

How important are the cementing bivalves in bioimmuration studies? Much of a Taylor's illustrated material (1990a,b) is derived from the attachment scars of oysters and indeed he rates this group along with the serpulids and cyclostome bryozoans amongst the finer bioimmuring organisms. Clearly the processes of cementation and bioimmuration are intimately related. It should therefore be possible, on the basis of work described in this thesis on the mechanism of cementation, to propose a feasible mechanism for bioimmuration.

Taylor (1990a), with reference to the excellent detail involved in oyster and bryozoan bioimmuration, comments on the extreme thinness of the outer organic layers,

periostracum and cuticle, respectively, reported for these taxa. Chapter 3 has already established how crucial the possession of a thin periostracum is to the construction of a valve which conforms to the microtopography of a substratum and demonstrated the high fidelity achievable between outer shell layers and that topography.

I have proposed two basic models by which bioimmuration may occur. These are discussed below along with the diagnostic features which could be used to distinguish between them. Figure 7.6 illustrates these models.

(i) *Periostracal wrapping*

In this model the periostracal sheet wraps around the obstruction onto which outer shell layers are then secreted. The morphology of the bioimmured organism is, therefore, taken up by the outer shell layers. The predictions of this model imply that it should be possible to determine the presence of the periostracal layer between the bioimmuration and the bioimmurer's shell. Where two folds of the periostracum meet around the obstruction, as illustrated in the inset of Figure 7.6(a), a double layer of periostracum should be visible. In the case of the bioimmurer being an oyster, as illustrated in Figure 7.6, it should be possible to recognise the terminal ends of the hexagonal prisms of the outer shell layer.

(ii) *Cement moulding*

This model predicts that the finest scale of bioimmuration is picked up in the extraperiostracal cement layer. Extrapallial fluid, leaked through the periostracum, nucleates on the surface of the bioimmured organism. If this model applies there should be no sign of the periostracum or of the terminal ends of the prisms.

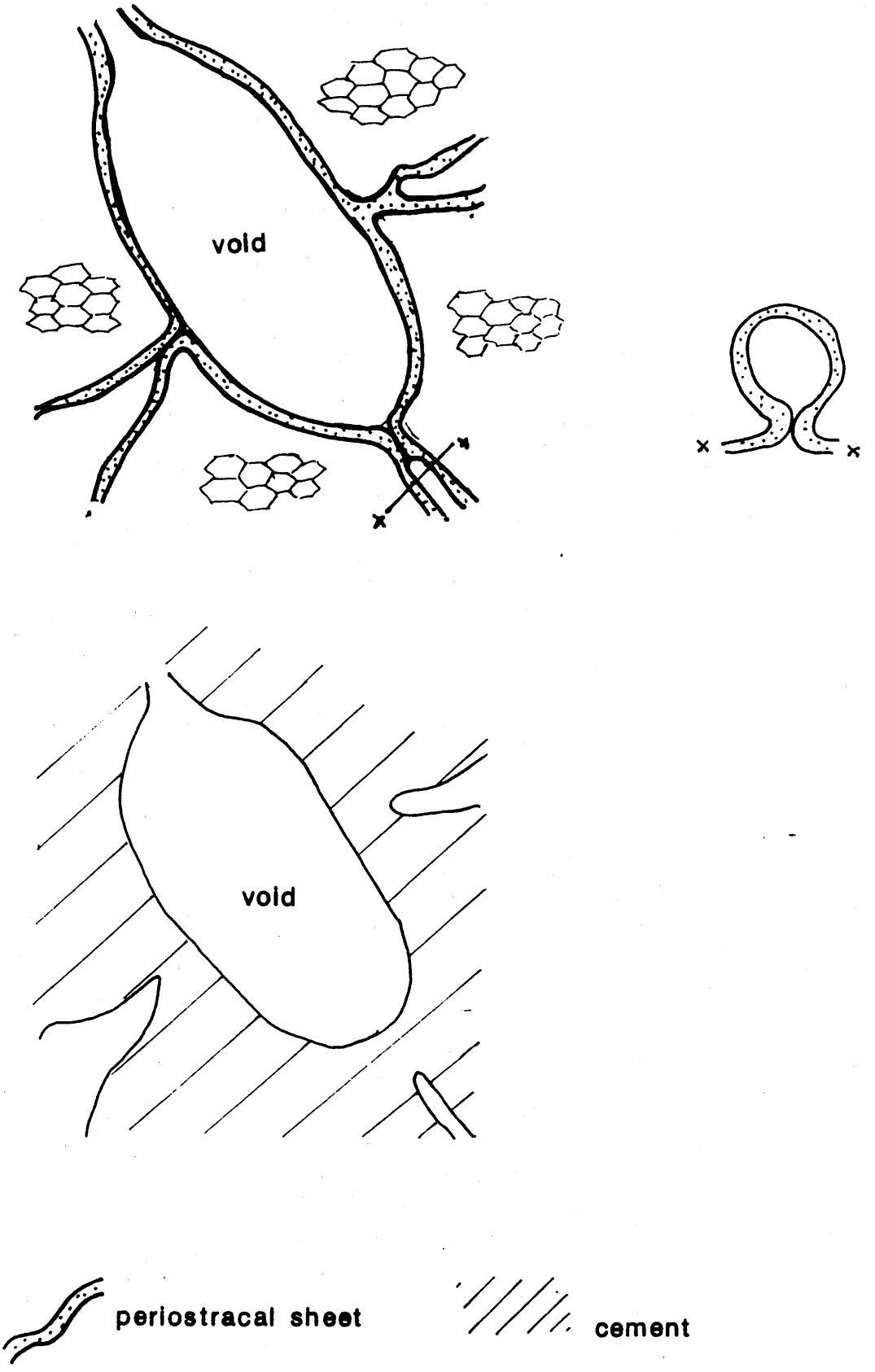


Figure 7.6: Models for the mechanism of bioimmuration. See text for explanations. Diagram based on Taylor (1990a) Plate 1, figure 4, of an oyster bioimmuring an ascophoran bryozoan.

It is undoubtedly true that periostracal wrapping plays some role in bioimmuration. Examination of oysters overgrowing barnacles shows that the outer prismatic layer very accurately mimics the outline of the balanoid. However, examination of Taylor's plates and a bioimmuring oyster, mounted as stubs EMH0260 and EMH0349, kindly given to me by PDT, suggests that this model is not sufficient to account for the finest bioimmurations. For example, in the plate from which Figure 7.6 was drawn there is no trace of the presence of a thin periostracal wrapping nor recognisable prisms in the sole of the oyster. My measurements of the dimensions of the terminal ends of prisms for Recent oysters suggest values of 10-15μm, figures which concur with values determined from micrographs of *Crassostrea virginica* published by Carriker, Palmer and Prezant (1980). Prisms of comparable dimensions should be readily identifiable. It is therefore postulated that much of the finer detail bioimmuration results from moulding in the extraperiostracal cement layer. It is also possible that in those bioimmurations which appear as casts, e.g. Taylor (1990b) Plate 2 Figure 6, the casting medium may be derived from the oyster cement .

It has been noted that there is a tendency for cemented bivalves to spall off their substrata during preparation. In many oysters the plane of weakness may be between the prisms and the cement (perhaps following the line of the organic rich periostracum). In these instances any bioimmuration apparent will have resulted from wrapping of the periostracum, and consequently the moulding will be of lower fidelity.

7.5 CEMENTATION IN OTHER TAXA

The mechanisms by which organisms biomineralise and the controls on these are recognised to be of fundamental importance in evolutionary processes. Cementation provides an excellent case study of biomineralisation and this research has elucidated the mechanisms, preadaptations and constraints involved in cementation in bivalves. However, this mode of life is not confined to this class. Members of the gastropods, crustaceans, brachiopods, bryozoans, cnidarians, sponges and even annelid worms

also firmly encrust hard substrata. It will be important to establish whether there are only a limited number of mechanisms by which organisms can cement. We must also discover whether increased predation resistance, which has been a key factor in the evolution of the habit in the bivalves, has been equally important in its evolution in other taxa.

Similar approaches are required to those used in this thesis. Of principal importance is establishing for each taxon whether the adhesion is the result of an 'organic glue' or a mineralised secretion. If mineralised, how does the manufacture of this cement relate to the organism's biomineralization processes?

Clark (1976) stresses that the biogenic precipitation of calcium carbonate must be isolated from the seawater to avoid the poisoning effects of magnesium ions. He lists three ways in which organisms achieve separation between the secreting surface and the external medium:

(i) *Periostracum*

A periostracal sheet isolates the tissue and the fluid from which the calcium carbonate crystallizes from the seawater. It also provides the template onto which the crystals nucleate. This is the mechanism employed by the molluscs, which is reviewed in Section 1.3.2.

(ii) *Marginal fold*

Growth of existing crystals occurs from a fluid, supersaturated with respect to calcium and carbonate ions, in a cavity enclosed by a flap of tissue. This is the method utilized by the corals (Constanz, 1986).

(iii) *Carbonate slurry*

Crystals of calcium carbonate are secreted by special 'calcium secreting glands' away from the site of hard part formation. These preformed crystals are transported to their eventual destination by a mucopolysaccharide secretion. Hard parts formed in this way, e.g. serpulid tubes, contain a very high proportion of organic material.

It will be interesting to determine how many of these mechanisms can be adapted to secrete a calcareous cement.

7.5.1 Interesting groups for further study

7.5.1.1 Cemented gastropods

The vast majority of gastropods are vagile, crawling on a muscular foot, but a very small number of this class are sessile, cemented to a hard substratum. These "worm snails", which bear an undeniable resemblance to serpulid worms, are uncoiled with highly irregular shells.

Members of three gastropod families employ this cemented mode of life: Vermetidae, Siliquariidae and some members of the Turritellidae . According to Bieler (Delaware Museum of Natural History, personal communication) the cemented habit has been independently evolved in each of these families. The literature on the cemented gastropods is very sparse, and I know of no publications dealing with their mechanism of attachment. Preliminary investigations on alcohol-preserved vermetids, supplied by Bieler, suggests a mineralised cement. Immersion in concentrated hypochlorite for over six months has failed to break the bond between shell and substratum. Time has not permitted further study, but this simple observation is very suggestive of a convergent mechanism with the cementing bivalves.

As members of the phylum Mollusca, the cementing gastropods share the same mode of valve secretion with the bivalves and hence the same mechanism of cementation may be feasible, by simple modification of the mantle and periostracum. Prompted by enquiries as to the nature of the periostracum of these gastropods, Bieler informs me that"..wormsnails have fairly thin periostraca" but notes that in one genus *Thylacodes* it is thicker. It does not appear that these values are known, but it would seem to suggest a great similarity to the bivalves.

7.5.1.2 Cementing brachiopods

Most brachiopods, living or fossil, attach epifaunally to either hard or soft substrata by means of a pedicle, a fleshy stalk derived from either one of the larval segments in articulates, or a posterior enlargement of the mantle in inarticulates (Rudwick, 1970). Yet the phylum has also adapted to exploit a number of other modes of life, such as burrowing in soft sediments (lingulids), and free living and cementation to hard substrata. These diverse life habits appeared early in the history of the phylum, all existing by the Silurian (Bassett, 1984).

The acquisition of cementation within the brachiopods has been polyphyletic (Rudwick, 1970), but there is some doubt as to the precise number of times the habit has evolved. Rudwick (1970) lists four separate instances but acknowledges that there may be more (1970, p.85). Certainly cementation has arisen separately in both articulate and inarticulate orders. A search of the literature has been undertaken to try and assess the known occurrences of the habit. The resultant information is shown in Figure 7.7.

Cementing Articulata

Following Cowen and Rudwick (1967), Rudwick (1970) contends that all cementing articulates belong to the order Strophomenida, in which there have been three independent appearances of the habit:

(i) Strophomenacea

A few members of this superfamily are recorded as having been cementers during the Silurian, including the earliest known cementing articulate *Liljevalia gotlandica.*

(ii) Davidsonacea

Members of the Davidsonacea evolved the cemented habit during the Devonian and later gave rise to the Lyttoniacea, and, according to Rudwick, the still extant Thecideacea.

INARTICULATA

Order Acrotretidae

Superfamily Craniacea (Ordovician-Recent)*

Superfamily Discinacea (Silurian-Recent)^

?Genus *Angarella* (Middle Ordovician) *

?Genus *Undiferina* (Ordovician)^

Order Lingulacea

Family Craniopsidae (Ordovician-Early Carboniferous)*

ARTICULATA

Order Strophomenida

Superfamily Strophomenacea (Silurian-Middle Carboniferous)*

Superfamily Davidsonacea (Devonian-Upper Permian)*

Superfamily Strophalosiacea (Devonian-Upper Permian)*

Order Atrypida

? (Devonian)*

Order Spiriferida

Superfamily Thecideacea (Upper Permian-Recent)*

*= calcareous valves ^=chitinophosphatic valves

Figure 7.7: Possible clades of cementing brachiopods and their stratigraphic ranges. Information has been culled from the literature, principally Rowell in Moore (1965), Rudwick (1970), Williams (1973) and Bassett (1984).

(iii) Strophalosiacea

The highly aberrant cementing richthofeniids, which were important components of some Late Palaeozoic reefs, derived from cementing Strophalosiacea which evolved during the Devonian.

It seems likely, however, that cementation has evolved in the articulates outside of the strophomenides. Rudwick (1970) based his decision that the enigmatic Thecideacea, including the extant genus *Lacazella,* belong to the strophomenides on similarity of the lophophore and on the very fact that they cement. The latter reasoning is, unfortunately, a rather circular argument. Williams (1973) argues on the basis of shell structure that they belong to the order Spiriferida, or perhaps to the Terebratulida. More recent literature on this enigmatic group, e.g. Pajaud (1973) and Baker (1989), seem to accept their membership of the spiriferids. If this taxonomic placing is correct then the thecidiacea certainly represent an independent occurrence of cementation, evolving in the Upper Permian and persisting to the present day.

Additionally, Bassett (1984) quotes Struve (1980) reporting a Middle Devonian cementing atrypacean (Order Atrypida). Here again, if correct, this would represent yet another independent acquisition of the cemented habit.

Cementing Inarticulata

Rudwick (1970) considers a single occurrence of cementation within the inarticulates; the Craniacea. This anomalous calcite secreting superfamily are first known to have cemented during the Ordovician and have remained extant to the Recent. However, there is evidence of other clades of cementing inarticulates. The *Treatise* (Moore, 1965) and Williams and Wright (1970) consider the Craniopsidae to belong to the Lingulacea, despite their convergence of habit and shell mineralogy with the Craniacea. Members of this family are recorded as cementing in the Ordovician and Silurian. Also Rowell in the *Treatise* (Moore, 1965) regards the previous placing of the Ordovician cementing genus *Angarella* within the Craniacea as doubtful.

Chitnophosphatic inarticulates are also capable of cementation. The Discinacea (Ordovician to Recent) have been cementing at least since the Silurian (Bassett,1984), and Rowell (in Moore, 1965) regards the Middle Ordovician genus *Undiferina* (Family Acrotretidae) as probably cementing.

There are clearly problems with identifying the number of clades of cementing brachiopods. As with the bivalves there are the problems caused by valve distortion and necessary anatomical rearrangement masking useful phylogenetic characters. Additionally, as pointed out by Cowen and Rudwick (1967) identifying fossil cementers may be hampered by poor preservation. Here post mortem distortion and breakage can be misidentified as attachment surfaces. New studies are required to document thoroughly the taxonomic and stratigraphic occurrences of the habit.

However, from the data, two important difference emerges in comparison with the cementing bivalves:

(i) The cemented brachiopods have failed to reach the diversity and abundance of the cemented bivalves. Occurrences of the habit are more sporadic and none of the clades has ever matched the success of the oysters or rudists.

(ii) Cementation in the brachiopods occured commonly and most frequently during the Palaeozoic. There was no 'sudden' emergence of cemented forms at the beginning of the Mesozoic as there was with the bivalves.

These differences pose a number of interesting questions. For example, have the brachiopods taken second place in terms of the cemented habit by the constraints of their own body plan, or have they been outcompeted by the bivalves, at least since the Mesozoic? Steele-Petrovic (1979) has already suggested that the general demise of the brachiopods, apparently coincident with the post-Palaeozoic radiation of the bivalves, is due to the superior flexibility of the latter's bodyplan, whilst Gould and Calloway (1980) contend that it is merely the result of the severity of the end Permian extinctions on the former. Also, does the cemented habit in the brachiopods afford any protection against predation?

Aside from the problems of recognising cementing brachiopods, previous work on the phylum has largely failed to address the biological problems of cementation. A number of important questions arise, similar to those expressed in Section 1.5 for the bivalves, regarding the mechanisms, preadaptations and selection pressures associated with cementation.

Williams and Wright (1970), in their work on the shell structure of the calcareous inarticulate *Crania,* suggest that adhesion of the pedicle valve is by a semi-fluid periostracum, i.e. a mucopolysaccharide glue. However they offer no direct evidence for this. Rudwick (1970, p.85) notes of all cemented brachiopods "The chemical nature of the cemented attachment, like that of the pedicle, is unknown; but it is very strong and survives fossilisation, and therefore presumably involves an intimate bond between the calcium carbonate of the shell and the material of the substrate.". I know of no other published discussions of the mechanism of cementation in brachiopods. There are, therefore, a number of important questions to be answered. There is a need to discover whether the bond is organic or mineralised and whether the same mechanism has been convergently evolved in each clade.

The brachiopods have an additional interest when compared to the study of cementation in bivalves. Whereas all bivalves have calcareous valves the brachiopod valves may be calcareous or chitinophosphatic. Although the majority of cementing brachiopods fall into the former category, some of the cementing inarticulates belong to the latter. Study of the mechanism of cementation in these chitinophosphatic forms will show whether there is convergence with the calcareous cementers or whether there has been a totally different innovation.

Presumably the process of cementation is intimately related to the valve secreting mechanism. Williams (1970) has described valve secretion in the Recent rhynchonellid *Notosaria.* According to Williams, the mechanism he describes is likely to be basically the same in all living articulates and to have remained little modified over geological time.

As with the bivalves, calcareous shell material is laid down by the mantle on to a mucopolysaccharide sheet, the periostracum. Despite this similarity to the molluscs, I perceive a fundamental difference between the two processes. In the brachiopods the system is essentially 'dry'; there are no reports of an equivalent to the extrapallial fluid between the mantle and periostracum. This would imply that the crystalline shell matter is secreted directly by the mantle epithelium rather than by the intermediacy of a supersaturated fluid. Since the leakage of the extrapallial fluid is pivotal to the mechanism of cementation in the bivalves, does the apparent lack of this fluid in the brachiopods mean that they cannot cement in this way?

7.6 FINAL COMMENT

Encrusting organisms present ideal subjects for evolutionary research. They possess remarkably complete stratigraphic records and their fixed nature preserves detail of ecological interactions, substrate relationships and ontogenetic changes. Although the cementing habit has convergently evolved in a large number of taxa little is known about the mechanisms, preadaptations and selection pressures which favour the acquisition. This study of cementation in bivalves has produced valuable information about the convergent evolution of cementation in one class. These results point the way for studying the phenomenon in other groups.

APPENDIX I
STUB DIRECTORY

All elecron microscope stubs are held in The Natural History Museum (London). The material is split into two collections. Recent specimens are deposited as the Harper Collection in NHZ, the fossil material in NHP.

Preparation
AD Air dried
CPD Standard CPD from live material in the manner described in Section 3.2.3
CPD† CPD from preserved material as detailed in Section 3.2.3
Fr Fractured and cleaned in an ultrasonic bath.
Et Fractured and etched in 10% Formic acid for 5-20 seconds.
Wash Washed in ultrasonic bath.
KOH Immersion in concentrated potassium hydroxide to remove organic material.
Ac- Immersion in 10% Formic acid to remove all calcareous material.
Ts- Thin section, uncovered.

All stubs have been gold sputtered, unless marked Ω to indicate carbon coating.

A: ZOOLOGICAL MATERIAL

Stub EMH0	Specimen	Preparation	Locality
12	*Ostrea edulis* -gill	CPD	Commercial
30	*Chlamys pusio*- R V mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
31	*Anomia ephippium*-R V mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
32	*Anomia ephippium*-R V mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
34	*Crassostrea gigas* -L V removed	CPD	Min.Ag.
35	*Anomia ephippium* Byssal apparatus	- CPD	Finnavara Point, Galway Bay. April 1988.
37	*Chlamys varia*- RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
38	*Chlamys varia*- RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
39	*Crassostrea gigas*-L V shell chip.	Et	Min.Ag.
40	*Anomia ephippium*-R V shell chip	Et	Finnavara Point, Galway Bay. April 1988.
41	*Anomia ephippium* -L V shell chip	Et.	Finnavara Point, Galway Bay. April 1988.
42	*Chlamys varia* - RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
43	*Chlamys pusio* - R V shell chip	Fr	Finnavara Point, Galway Bay. April 1988.
44	*Anomia* plug LS	Et	Finnavara Point, Galway Bay. April 1988.
45	*Anomia plug* - TS	Et	Finnavara Point, Galway Bay. April 1988.
46	*Crassostrea gigas* (6 week) attached to glass.	CPD	Min.Ag.
49	*Ensis* periostracum	AD	Brodick Bay, Arran
50	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
51	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.

52	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
53	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
54	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
55	*Chlamys pusio* - RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
56	*Chlamys pusio* - RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
57	*Anomia ephippium* mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
58	*Chlamys pusio* - RV mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
59	*Chlamys varia* - RV mantle mragins	CPD	Finnavara Point, Galway Bay. April 1988.
60	*Modiolus modiolus* - periostracum.	AD	ex NHZ
61	*Mytilus galiprovincialis* - periostracum	AD	ex NHZ
62	*Ostrea edulis* - RV mantle margins	CPD	Commercial
63	*Chlamys opercularis* - RV mantle margins	CPD	Millport
64	*Chlamys opercularis* - RV mantle margins	CPD	Millport
65	*Ostrea edulis*- LV mantle and gills	CPD	Finnavara Point, Galway Bay. April 1988.
66	*Ostrea edulis* - LV gills	CPD	Finnavara Point, Galway Bay. April 1988.
67	*Ostrea edulis*- adductor muscle	CPD	Finnavara Point, Galway Bay. April 1988.
68	*Ostrea edulis*- adductor muscle	CPD	Finnavara Point, Galway Bay. April 1988.
69	*Ostrea edulis*- L V mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
70	*Chlamys opercularis* - RV mantle margins	CPD	Millport
71	*Chlamys opercularis* - RV mantle margins	CPD	Millport
72	Periostraca of *Ostrea Ensis* and *Arctica*	AD	ex NHP
73	Periostracum of *Solen*	AD	ex NHP
74	Periostraca of *Laevicardium, Lutraria* and *Hiatella*	AD	ex NHP
75	*Chlamys pusio* - RV shell fragment	Fr	Finnavara Point, Galway Bay. April 1988.
76	*Chlamys pusio* - RV shell fragment	Fr	Finnavara Point, Galway Bay. April 1988.
77	*Chlamys varia* - RV shell fragment	Fr	Finnavara Point, Galway Bay. April 1988.
78	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
100	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
101	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
102	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.

103	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
104	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
105	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
106	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
107	Flange from *Spondylus americanus*	Fr	Commercial
108	*Mercenaria mercenaria* - RV mantle margins	AD	Commercial
109	*Mercenaria mercenaria* - exhalant siphon	CPD	Commercial
110	*Mercenaria mercenaria* gill	CPD	Commercial
111	*Mercenaria mercenaria*-RV mantle margins	CPD	Commercial
112	*Mercenaria mercenaria* RV mantle margins	CPD	Commercial
113	*Mercenaria mercenaria* RV mantle margins	CPD	Commercial
114	*Mercenaria mercenaria* RV mantle margins	CPD	Commercial
115	*Monia squama* RV shell fragment	Fr	Oban
116	*Chlamys pusio*- RV shell fragment	Fr	Finnavara Point, Galway Bay. April 1988.
117	*Mytilus edulis*- foot	CPD	Oban
118	*Mytilus edulis*-byssal threads	CPD	Oban
119	*Mytilus edulis*- RV mantle margins	CPD	Oban
120	*Mytilus edulis*- shell	CPD	Oban
121	*Modiolus modiolus* - RV mantle margins	CPD	Oban
122	*Modiolus modiolus* - RV mantle margins	CPD	Oban
124	*Spondylus butleri* flange	Fr	Commercial
125	*Spondylus butleri* flange	Fr	Commercial
126	*Perna viridis* - periostracum	AD	ex NHZ
127	*Anomia ephippium* plugs	AD	Finnavara Point, Galway Bay. April 1988.
128	*Anomia ephippium* plugs	Fr	Finnavara Point, Galway Bay. April 1988.
129	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
130	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
131	*Anomia ephippium* - mantle margins	CPD	Finnavara Point, Galway Bay. April 1988.
133	*Ostrea edulis*- attached valve	WASH	Finnavara Point, Galway Bay. April 1988.
134	*Monia squama* R V mantle margins	CPD	Oban
135	*Monia squama* R V mantle margins	CPD	Oban
136	*Mytilus edulis* mantle and shell	CPD	Oban

137	Attachment scar of oyster	WASH	Given by Paul Taylor
140	*Ostrea edulis* LV shell fragment	Fr	Commercial
141	*Monia squama* shell fragment	CPD	Oban
142	*Modiolus modiolus* R V mantle margins	CPD	Oban
144	*Pecten maximus* R V mantle margins	CPD	Oban
153	*Monia squama* -RV shell fragment	WASH	Oban
158	*Spondylus gaederopus* RV mantle margins	CPD	Commercial
159	*Spondylus gaederopus* RV mantle margins	CPD	Commercial
160	*Spondylus gaederopus* RV mantle margins	CPD	Commercial
161	*Crania* attached to *Modiolus modiolus*	Fr	Oban
162	*Spondylus gaederopus*- LV mantle margins	CPD	Commercial
163	*Spondylus gaederopus*- LV mantle margins	CPD	Commercial
164	*Crassostrea angulata* LV mantle margins	CPD	Oban
165	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
166	*Plicatula imbricata*- LV mantle margins	CPD†	ex NHZ
167	*Arctica islandica* -R V mantle margins	CPD	Oban
168	*Glycymeris glycymeris* - RV mantle margins	CPD	Oban
169	*Scrobicularia plana* -RV mantle margins	CPD	Oban
170	*Astarte elliptica* - R V mantle margins	CPD	Oban
171	*Venerupis decussata* RV mantle margins	- CPD	Oban
172	*Spondylus gaederopus* - LV mantle margins	CPD	Commercial
174	*Venerupis rhomboides* -- RV mantle margins	CPD	Oban
175	*Spondylus gaederopus* - LV mantle margins	CPD	Commercial
176	*Venus casina* -R V mantle margins -	CPD	Oban
177	*Plicatula imbricata*- RV mantle margins	CPD†	ex NHZ
178	*Thracia* - RV mantle margins	CPD	Oban
179	*Dosinia exoleta* - R V mantle margins	CPD	Oban
180	*Crassostrea angulata* - RV mantle margins	CPD	Oban
181	*Chlamys opercularis*- RV mantle margins	CPD	Oban
182	*Cerastoderma edule* - RV mantle margins	CPD	Oban
183	*Mytilus edulis* - R V mantle margins	CPD	Oban

184	*Modiolus modiolus* - RV mantle margins	CPD	Oban
185	*Ostrea edulis* - R V mantle margins	CPD	Oban
186	*Spondylus gaederopus* - RV mantle margins	CPD	Commercial
187	*Ostrea edulis* - L V mantle margins	CPD	Oban
188	*Chama* mantle margins	CPD	Commercial
189	*Chama* mantle margins	CPD	Commercial
193	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
194	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
195	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
196	*Cerastoderma edule* - RV mantle margins	CPD	Oban
197	*Cleidothaerus albidus* RV mantle margins	CPD†	New Zealand, donated by Ponder
198	*Cleidothaerus albidus* RV mantle margins	CPD†	New Zealand, donated by Ponder
199	*Myochama anomioides* - RV mantle margins	CPD†	Australia, donated by Ponder
200	*Myochama anomioides* - RV mantle margins	CPD†	Australia, donated by Ponder
201	*Saccostrea* LV mantle margins	CPD†	Thailand, donated by JDT
204	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
205	*Crassostrea gigas* (6 week) attached to glass.	CPD	Min.Ag.
206	*Scrobicularia plana* - RV mantle margins	CPD	Oban
207	*Glycymeris glycymeris* - RV mantle margins	CPD	Oban
208	*Dosinia exoleta* - RV mantle margins	CPD	Oban
209	*Venerupis rhomboides* - RV mantle margins	CPD	Oban
210	*Venerupis decussata* - RV mantle margins	CPD	Oban
211	*Monia squama* shell fragment	Fr	Oban
212	*Chlamys pusio* whole RV	WASH	Port Erin
214	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
216	*Chlamys pusio* - L V mantle margins	CPD	Port Erin
217	*Chlamys pusio* - R V mantle margins	CPD	Port Erin
218	*Chlamys pusio* - juvenile shell	WASH	Port Erin
219	*Chlamys varia* - LV mantle margins	CPD	Port Erin
220	*Chlamys varia* - RV mantle margins	CPD	Port Erin
221	Fractured RV of *Chlamys pusio*	Fr	Port Erin

222	Byssal notch of *Chlamys pusio*	WASH	Port Erin
232	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
233	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
234	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
235	RV of *Anomia ephippium* and *Monia squama*	Fr	Oban
236	*Cleidothaerus albidus* - attached valve	Fr	New Zealand, donated by Ponder
237	*Myochama* attached to *Glycymeris*	Fr	Australia, donated by Ponder
238	*Dimya* attached to bone	Fr	Donated by Morton
241	*Dimya* attached to bone	Fr	Donated by Morton
243	*Saccostrea* LV mantle margins	CPD†	Thailand, donated by JDT
249	*Dimya* attached to bone	Fr	Donated by Morton
250	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
251	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
252	*Hinnites giganteus* 8-10 months	WASH	Canadian fisheries
254	*Glycymeris kepelliana* RV shell fragment	Fr	Australia, donated by Ponder
256	*Hinnites giganteus* 8-10 months	WASH	Canadian fisheries
258	*Unio* shell	Fr	Stanton Harcourt, Oxfordshire
260	Base of attached oyster	WASH	Donated by Paul Taylor
266	*Lopha cristagli* -LV shell fragment	Fr	Commercial
268	*Etheria elliptica* Shell fracture	Fr	MNHN
269	*Etheria elliptica* Shell fracture	Fr	MNHN
270	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
271	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
272	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
273	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
274	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
277	Base of LV *Ostrea edulis*	WASH	Galway
278	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
279	*Hinnites giganteus* -RV mantle margins	CPD	Canadian fisheries
280	*Spondylus* attached to coral	Fr	Commercial
282	*Etheria elliptica* mantle margins	CPD	MNHN
286	*Etheria elliptica* mantle margins	CPD	MNHN

288	*Saccostrea* attached to bark	Fr	Thailand, donated by JDT
289	*Saccostrea* attached to bark	Fr	Thailand, donated by JDT
292	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
293	*Crassostrea gigas* (6 week) attached to calcite .	Fr	Min.Ag.
310	*Eucrassatella kingicoal* shell fractuire	Fr	ex NHZ
311	*Myochama* attached to *Eucrassatella*	Fr	ex NHZ
312	*Myochama* attached to *Eucrassatella*	Fr	ex NHZ
313	*Myochama* RV bleached off *Eucrassatella*	KOH	ex NHZ
316	Larval shell of *Cleidothaerus albidus*	WASH	New Zealand, donated by Ponder
317	RV attached *Dimya*	Fr	Hong Kong, donated by Morton
318	RV attached *Dimya*	Fr	Hong Kong, donated by Morton
321	*Myochama* attached to *Glycymeris*	Fr	South Australia, donated by Ponder
322	*Myochama* attached to *Glycymeris*	Fr	South Australia, donated by Ponder
323	*Arca tetragona* periostracum	AD	ex NHP
324	*Etheria elliptica* attached valve mantle margins	-CPD†	MNHN
325	*Etheria elliptica* attached valve mantle margins	CPD†	MNHN
326	*Etheria elliptica* unattached valve mantle margins	CPD†	MNHN
333	*Etheria elliptica* attached to substratum	Fr	MNHN
334	*Etheria elliptica* attached to substratum	Fr	MNHN
335	*Myochama* juvenile shell	WASH	South Australia, donated by Ponder
336	*Spondylus gaederopus* juvenile shell	WASH	Commercial
337	Decalcified periostracum of *Cleidothaerus*	Ac	New Zealand, donated by Ponder
338	*Hinnites gigateus* LV mantle margins	CPD	Canadian fisheries
339	*Hinnites giganteus* LV mantle margins	CPD	Canadian fisheries
340	Attached *Cleidothaerus*	Fr	New Zealand, donated by Ponder
341	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
342	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
343	*Crassaostrea gigas* LV - 2 weeks, bleached off substratum	KOH	Min.Ag.
344	*Crassostrea angulata*- LV mantle margins	CPD	Commercial - Courseuilles, Normandy
345	*Crassostrea angulata*- RV mantle margins	CPD	Commercial - Courseuilles, Normandy

347	Decalcified periostracum of *Etheria elliptica*, Unattached valve	Ac	MNHN
349	Underside of LV attachment scar, *Ostrea*	WASH	Donated Paul Taylor, Piran
350	Attachment scar of *Chama*	WASH	Commercial
351	Attachment scar of *Chama*	WASH	Commercial
352	Attachment scar of *Chama*	WASH	Commercial
353	*Etheria* attached	Fr	MNHN
354	*Crassostrea gigas* LV mantle margins	CPD	Commercial
355	*Crassostrea gigas* LV mantle margins	CPD	Commercial
356	*Crassostrea gigas* LV mantle margins	CPD	Commercial
357	*Crassostrea gigas* LV mantle margins	CPD	Commercial
358	*Crassostrea gigas* RV	WASH Ω	Seasalter shellfisheries, Kent
359	*Spondylus histrix* attached to coral	Ts	Commercial
360	Attached *Etheria eliptica*	Fr	MNHN
361	*Saccostrea* attached to mangrove wood	Fr	Thailand, donated by JDT
363	*Astarte elliptica* - RV mantle margins	CPD	Millport
364	*Ostrea edulis* - RV mantle margins	CPD	Millport
365	*Gari* - RV mantle margins	CPD	Millport
366	*Pseudamussium septemradiata* - RV mantle margins	CPD	Millport
367	*Chamalea* - RV mantle margins	CPD	Millport
368	*Nucula nitida* - whole animal, LV removed	CPD	Millport
369	*Abra alba* - RV mantle margins	CPD	Millport
370	*Chlamys pusio* - RV mantle margins	CPD	Port Erin
371	*Acanthocardia* - RV mantle margins	CPD	Millport
373	*Limaria hians* - RV mantle margins	CPD	Millport
374	*Modiolarca* - RV mantle margins	CPD	Millport
375	*Angulus tenuis* - RV mantle margins	CPD	Millport
376	*Nucula sulcata* - RV mantle margins	CPD	Millport
377	*Hiatella* - RV mantle margins	CPD	Millport
378	*Astarte sulcata* - RV mantle margins	CPD	Millport
379	*Mya arenaria* - RV mantle margins	CPD	Millport
380	*Lutraria lutraria* - RV mantle margins	CPD	Millport

395	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
396	*Myochama* attached to *Eucrassatella*	Fr	S.Australia, donated by Ponder
397	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
398	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
399	*Crassostrea gigas* (6 week) attached to glass.	Fr	Min.Ag.
400	RV *Chlamys varia*	KOH	Galway Bay
401	RV *Corbula gibba*	KOH	Millport
402	RV *Spondylus gaederopus*	KOH	Commercial
403	RV *Nucula sulcata*	KOH	Millport
404	RV *Hiatella*	KOH	Millport
405	RV *Chama lazarus*	KOH	Commercial
407	Decalcified periostracum of *Etheria elliptica*	Ac	MNHN
413	*Chlamys pusio* attachment scar	KOH	ex NHZ
415	RV *Cleidothaerus albidus*	KOH	New Zealand, donated by Ponder
416	RV*Astarte eliptica*	KOH	Millport
417	RV *Lima hians*	KOH	Millport
418	Rv *Unio*	KOH	Stanton Harcourt, Oxfordshire
419	RV *Mytilus edulis*	KOH	Oban
420	RV *Modiolus modiolus*	KOH	Oban

BM STUBS refer to a number of mounted specimens of air dried periostracum collected from NHZ specimens, chiefly Mytilacea and Arcacea. These are labelled individually.

B: PALAEONTOLOGICAL SPECIMENS

Stub EMH0	Specimen	Preparation	Locality
123	Anomiid plugs attached to *Isognomon.*	WASH	Upper Jurassic, Portugal. Donated by Fürsich.
137	*Pycnodonte* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
138	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
147	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
148	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
149	*Eonomia timida* attached to gryphaeid.	Fr	ex OUM cut from paratype JZ1784. Vaches Noires, Oxfordian.
150	*Lopha gregarea*	Fr	Vaches Noires, Upper Oxfordian
152	*Lopha gregarea*	Fr	Vaches Noires, Upper Oxfordian
154	Oyster attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
155	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
156	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
157	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
190	*Lopha* attached to *Plagiostoma*	Fr	St. Aubin sur mer, sponge reef, Middle Bathonian

137	*Pycnodonte* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
138	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
147	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
148	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
149	*Eonomia timida* attached to gryphaeid.	Fr	ex OUM cut from paratype JZ1784. Vaches Noires, Oxfordian.
150	*Lopha gregarea*	Fr	Vaches Noires, Upper Oxfordian
152	*Lopha gregarea*	Fr	Vaches Noires, Upper Oxfordian
154	Oyster attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
155	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
156	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
157	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
190	*Lopha* attached to *Plagiostoma*	Fr	St. Aubin sur mer, sponge reef, Middle Bathonian
191	*Atreta* attached to *Plagiostoma*	Fr	St. Aubin sur mer, sponge reef, Middle Bathonian
202	*Atreta* attached to *Plagiostoma*	Fr	St. Aubin sur mer, sponge reef, Middle Bathonian
203	*Atreta* attached to *Echinocorys*	Fr	ex Hammond Collection (Cambridge) Overstrand, Maastrichtian
213	*Atreta*	WASH	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
215	*Spondylus* attached to *Inoceramus.*	Fr	Campanian of Arkansas, donated by W.J. Kennedy
223	*Spondylus* attached to *Echinocorys*	Fr	Holtug quarry Stevns Klint, Denamark, Upper Maastrichtian
224	*Pycnodonte* attached to *Echinocorys*	Fr	ex Hammond Collection (Cambridge) Overstrand, Maastrichtian
225	*Lopha gregarea* pair	Fr	Vaches Noires, Upper Oxfordian
226	*Plicatula fistulosa* attached to gryphaeid	Fr	Vaches Noires, Upper Oxfordian
227	*'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian
228	*'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian
229	*Spondylus consobrinus* attached to sponge	WASH	St. Aubin sur mer, sponge reef, Middle Bathonian
270	*Exogyra sp.*	WASH	Rainville cement works, Normandy, Cornbrash
271	*Eonomia timida* attached to gryphaeid	Fr	Vaches Noires, Upper Oxfordian
275	*Atreta* attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
276	Oyster attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
301	*Spondylus consobrinus* attached to sponge	WASH	St. Aubin sur mer, sponge reef, Middle Bathonian
307	Anomiid plugs attached to *Isognomon.*	WASH	Upper Jurassic, Portugal. Donated by Fürsich.
314	*Atreta* attached to *Plagiostoma*	Fr	St. Aubin sur mer, sponge reef, Middle Bathonian

315	*Atreta* attached to phosphatic nodule	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
320	*Atreta* attached to phosphatic nodule	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
329	*Liostrea hebridica*	Fr	Locality unknown, donated by D.M. Martill. Great Estuarine
330	Juvenile portion of *'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian
331	*'Eopecten B'*	Fr	Campagnettes Quarry, Normandy, Bathonian
348	*'Eopecten B'*	Fr	Campagnettes Quarry, Normandy, Bathonian
391	*Atreta* attached to *Echinocorys*	Fr	ex Hammond Collection (Cambridge) Overstrand, Maastrichtian
392	Oyster attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
393	Oyster attached to *Inoceramus*	Fr	Munday's Hill Pit, Leighton Buzzard. Gault (Albian).
394	Cluster of *Hippurites socialis*	TS	ex Skelton Collection, Piolenc, France, Lower Santonian
406	Oyster spat on the base of adult oyster	WASH	M40 extension, Oxfordian
408	*'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian
409	*'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian
410	*'Eopecten B'*	Fr	Campagnettes Quarry, Normandy, Bathonian
411	*'Eopecten B'*	Fr	Campagnettes Quarry, Normandy, Bathonian
412	*'Eopecten A'*	Fr	Campagnettes Quarry, Normandy, Bathonian

APPENDIX 2

SHELL MICROSTRUCTURES

During the course of this study a large number of sections through the attached valves of cementing bivalves have been investigated. Although the seminal work of Taylor et al. (1969a) has already covered the microstructures of most of these taxa, it is now twenty years since that work was done. Higher resolutions are now possible and I have also had the opportunity to examine taxa such as *Dimya, 'Eopecten'* and *Atreta* which were unstudied by the original authors.

The initial reason for recording the shell structures observed in the cemented valve was to search for any possible link between shell microstructure and the cemented habit. No such correlation is apparent. Cementing bivalves display a wide range of shell structures from the most primitive molluscan shell structure (aragonitic nacre and prisms) to the derived structure of the Ostreacea, with their almost entirely calcitic mineralogy with principally foliated structure. Although most of the cementing taxa possess an outer prismatic shell layer it is not universal. Prisms are conspicuously absent in the Dimyacea, Spondylidae and most *Chama*. A large number of the clades do have a large proportion of foliated shell but this is hardly surprising; Taylor and Layman (1972) have found that foliate shell structure is exclusive to the epifaunal bivalves, whether cementing or otherwise.

The information given overleaf has been derived from SEM studies of fractured or etched specimens and thin sections. No attention has been given to the myostracal layers.

It has not been possible to make observations for members of the Terquemiidae, Lithiotidae, Chondrodontidae or pseudomonotids. However, Newell and Boyd (1970) refer to the pseudomonotids as possessing an outer prismatic layer.

KEY

CALCITE

= PRISMATIC

= FOLIATED

= CROSS LAMELLAR

ARAGONITE

= PRISMATIC

= COMPLEX CROSS LAMELLAR

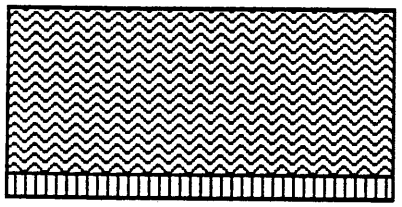
= CROSS LAMELLAR

= NACRE

STRUCTURE
Outer shell layer is at the base of each rectangle

COMMENTS

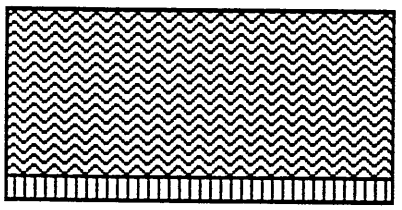
OSTREIDAE



Specimens examined: Ostrea edulis EMH0133 Crassostrea gigas EMH0100-106, Saccostrea cucullata: EMH0201, Lopha cristagalli: EMH0266.

Contrary to Taylor et al. (1969) outer prismatic layer is present. No pallial myostracum.

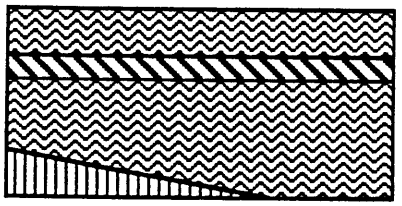
GRYPHAEIDAE



Pycnodonte (Chalk) EMH0224

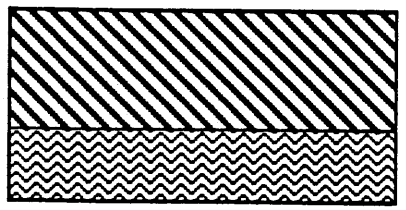
Details as above.

PECTINIDAE



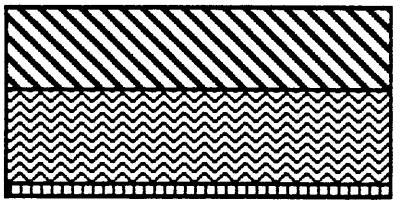
Chlamys pusio:EMH0076, C.varia: EMH0077, C. opercularis: EMH0075 and 'Eopecten': EMH0408 -00412..
Prismatic outer shell layer only present in more juvenile stages.

SPONDYLIDAE



Spondylus histrix: EMH0359, S. gaederopus: EMH0186 S. butleri: EMH0124, 0125, S.americanus: EMH0107.

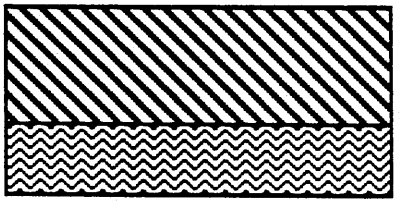
PLICATULIDAE



Plicatula imbricata: EMH0166, P. fistulosa; EMH0226

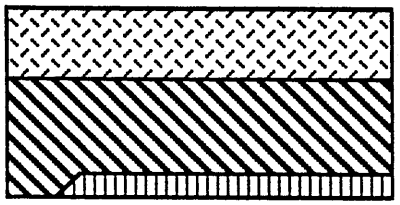
Waller (1978) comments that the outer prismatic layer is not always present.

DIMYIDAE



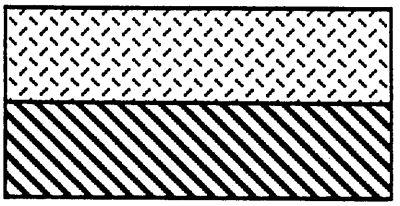
Dimya sp. EMH0249, Atreta EMH0155, 156
Yonge (1978b) refers to an outer prismatic layer, but Waller (1978) notes its absence.
The shell structure of Gault Atreta appears identical to that of modern dimyids.

'RUDISTS'



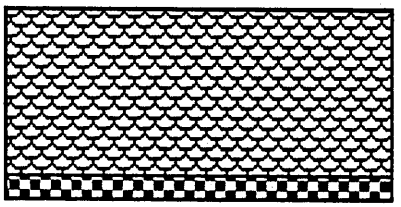
Data taken from Skelton (1978).
No pallial myostracum.

CHAMACEA



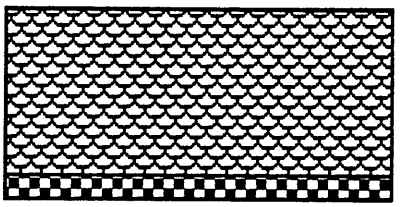
Chama sp.: EMH0351.
Kennedy, Morris and Taylor (1970) note that Chama pellucida and C. exogyra are atypical in the possession of a thin calcitic outer prismatic shell layer.

MYOCHAMIDAE



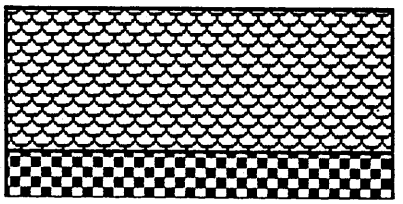
Myochama anomioides: EMH0199, EMH0200 EMH0237.

CLEIDOTHAERIDAE



Cleidothaerus albidus: EMH0236.
Outer prismatic layer varies markedly in thickness.

ETHERIIDAE



Etheria elliptica: EMH0268, 0269.
Taylor et al (1969) acknowlege the presence of a thin outer prismatic layer in other Unionacea but failed to find it in etheriids.

APPENDIX 3

PALLIAL LINE INSET DATA

Data derived in the manner described in 4.2.2. Most measurements have been derived from specimens in The Natural History Museum. Individual specimens are not identified for two reasons. Firstly in most cases the specimens are part of lots not individually numbered, and secondly, because it is hoped in the very near future to develop a more precise method of recording this type of data, e.g. by digitising. In event of such a development new figures will be published.

PART I: RECENT DATA

ARCACEA

Arca indica: 0.22, 0.18
Arca scimanensis: 0.11
Anadara antiquata: 0.08
Anadara tetragona: 0.07,0.06,0.07,0.04,0.05,0.03
Arca tortuosa: 0.07, 0.08

LIMOPSACEA

Axinactica glycymerella: 0.07
Glycymeris keppeliana: 0.14,0.15,0.16,0.12
Glycymeris multicostata: 0.09,0.11,0.07
Limopsis indica: 0.11,0.1,0.13
Limpopsis multistriata: 0.13,0.17,0.12,0.11
Limopsis tajimae: 0.11

MYTILACEA

Adula californiensis: 0.08, 0.09
Aulacomya magellanicus: 0.06,0.11,0.1,0.09,0.1,0.13,0.13,0.17,0.07
Aulacomya maorianus: 0.11,0.11,0.12,0.09
Geukensia demissa: 0.1,0.1,0.08,0.09,0.08,0.08,0.08,0.09,0.1,0.12
Lithophaga antillarum : 0.05,0.04,0.04,0.04
Lithophaga lithophaga: 0.05,0.05,0.03,0.03,0.03,0.04,0.04,0.05,0.06
Lithophaga nigra: 0.03,0.02,0.03
Lithophaga teres: 0.01,0.01,0.02,0.06,0.07,0.03
Modiolus adriacticus: 0.07,0.09,0.09,0.09,0.09,0.09,0.09,0.08,0.08,0.07,0.08
Modiolus albicosta: 0.07,0.14,0.12,0.09
Modiolus aureolatus: 0.08,0.11,0.07,0.1,0.08
Modiolus auriculatus: 0.09,0.11,0.15,0.11
Modiolus barbatus: 0.1,0.07,0.09,0.08,0.11,0.07,0.09,0.1,0.11,0.09
Modiolus impactus: 0.07,0.06,0.07,0.09,0.09,0.09
Modiolus modiolus: 0.1,0.12,0.13,0.12,0.11,0.12,0.1,0.13,0.11,0.1,0.12,0.08,0.13
Modiolus niger: 0.15,0.14,0.1,0.15
Modiolus phillipinarum: 0.1,0.11,0.1
Modiolus varicosa: 0.06,0.06,0.06
Mytilus californiensis: 0.12,0.09,0.1,0.09,0.1,0.11,0.11,0.11,0.1,0.8
Mytilus edulis: Raw data presented in Figure 4.7.
Perna perna: 0.12,0.12,0.08,0.13,0.13,0.12,0.12,0.17,0.15,0.15,0.16
Perna viridus: 0.16,0.18,0.18,0.15,0.12,0.14,0.16,0.13, 0.18, 0.15, 0.17,0.15
Septifer bilocularis: 0.09,0.14,0.11,0.08,0.11,0.12,0.11,0.08,0.07,0.1
Stavelia torta: 0.07,0.08,0.06,0.07,0.08,0.11,0.05,0.08,0.07,0.09
Trichomya hirsutus: 0.11,0.09,0.11,0.1,0.11

ANOMIACEA

Anomia ephippium: 0.36,0.4,0.42
Monia squama: 0.41,0.51

PECTINACEA
Amussium: 0.25
Chlamys caurinus: 0.4
Chlamys magellanicus: 0.23
Chlamys opercularis: 0.27
Chlamys pusio: 0.3,0.3,0.31,0.32,0.32,0.36,0.32,0.32,0.33,0.44,0.34,0.35,0.35,0.35, 0.37 ,0.33,0.35,0.36,0.32,0.36,0.36,0.36,0.33,0.25
Chlamys varia: 0.21,0.22,0.26,0.23,0.26,0.22,0.25,0.27,0.24,0.26, 0.27,0.25,0.26,0.25, 0.24,0.26,0.25,0.3,0.24,0.25,0.26,0.23,0.27,0.26,0.25,0.23,0.26,0.19,0.33,0.23,0.26, 0.22, 0.23,0.27
Chlamys zealandiae: 0.22,0.28
Hinnites giganteus: 0.33,0.32,0.31,0.27,0.23,0.3,0.27,0.24,0.32,0.35,0.32,0.35,0.23,0.28
Lyropecten nodosus: 0.23
Patinopecten caurinus: 0.4,0.37
Pecten flexuosus: 0.21,0.32
Pecten jacobeaus: 0.32,0.31,0.48,0.34,0.36,0.49,0.36,03
Pecten maximus: 0.37,0.36,0.31
Pecten pensis: 0.3
Pecten ziczac: 0.32
Spondylus aurantius: 0.27,0.27,0.26
Spondylus ducalis: 0.18,0.22,0.2,0.21,0.19,0.2
Spondylus gaederopus: 0.29,0.29,0.32,0.31,0.29,0.29,0.31,0.29,0.28,0.3,0.34,0.26, 0.23,0.21,0.29,0.26,0.28,0.22,0.23,0.23,0.23
Spondylus hystrix: 0.3,0.3
Spondylus imperialis: 0.29,0.25,0.22,0.29,0.22
Spondylus pacificus: 0.28
Spondylus pesasinius: 0.25, 0.25, 0.25,0.26,0.25
Spondylus princeps: 0.28,0.29,0.32,0.27,0.32,0.27,0.26
Spondylus powelli: 0.38,0.2
Spondylus regius: 0.23,0.26,0.26
Spondylus sinensis: 0.25,0.25,0.2,0.23
Spondylus varius: 0.28,0.28, 0.3

PLICATULACEA
Plicatula australis: 0.17
Plicatula depressa: 0.18
Plicatula imbricata: 0.23,0.19,0.15
Plicatula philippinarum: 0.23,0.18,0.19
Plicatula plicata: 0.18,0.16,0.15
Plicatula ramosa: 0.17,0.22,0.24,0.29,0.24,0.32,0.23,0.1
Plicatula simplex: 0.18

DIMYACEA
Dimya corrugata: 0.29,0.31,0.31,0.38
Dimya japonica: 0.21
Dimya maoriana: 0.21

OSTREACEA
Alectronella: 0.54,0.49
Crassostrea angulata: 0.38,0.38,0.24,0.23,0.3,0.45,0.49,0.37,0.39,0.42
Crassostrea gigas: 0.3,0.31,0.26,0.42
Crassostrea virginica: 0.37,0.38,0.32,0.26,0.29,.34
Lopha crystaglii: 0.47,0.38
Ostrea edulis: 0.37,0.4,0.44,0.27,0.39,0.49,0.47,0.43,0.4,0.45,0.41,0.39,0.4.
Saccostrea cucullata: 0.11
Striostrea multistriata: 0.39,0.4

UNIONACEA
Acostaea lobata: 0.35,0.27,0.24,0.23, 0.32
Alathyria: 0.21,0.18, 0.18,0.18,0.18
Amblema trapezoides: 0.21

Anodonta chariazana: 0.16,0.18
Aspatharia bellamyi: 0.17,0.18
Aspatharia dahomeynsis: 0.14,0.15
Aspatharia pfiefiena: 0.13, 0.13
Aspatharia rubens: 0.15,0.16,0.15,0.16
Aspatharia sinuata: 0.16,0.15,0.19,0.18
Bartlettia steffani: 0.37
Cameroni spekei: 0.21
Etheria elliptica: 0.37,0.37,0.31,0.36,0.38,0.4,0.37,0.36,0.35,0.4,0.34,0.39,0.29,0.36, 0.48, 0.27,0.37,0.37,0.37,0.39,0.35,0.38,0.19,0.34,0.39,0.32,0.32,0.27,0.48,0.25
Grandiddieria rostrata: 0.18,0.18
Hyridella drapela: 0.13
Mutela dubia: 0.11,0.17,0.13,0.19,0.17
Pleidon ovatus: 0.16, 0.19
Quadrula lachrymosa: 0.11
Quadrula plicata: 0.19
Quadrula tuberculata: 0.15
Spatha kariensis: 0.16
Unio bakeri: 0.14,0.22
Unio tertioscules: 0.17,0.17
Unio tradiana: 0.18,0.18,0.2
Velesunio ambiguis: 0.15,0.12,0.12

TRIGONIACEA
Neotrigonia: 0.28,0.27

LUCINACEA
Codakia divergens: 0.29
Codakia tigerina: 0.07,0.07,0.1,0.13,0.09,0.11,0.13,0.14
Lucina gemma: 0.17
Phacoides argenteus: 0.15
Phacoides dentifer: 0.12,0.25,0.17,0.18,0.18
Phacoides jamaiciensis: 0.11,0.1,.1,0.11
Phacoides nutalli: 0.16,0.15,0.14
Phacoides pectina: 0.1

CHAMACEA
Chama coralloides: 0.12,0.16
Chama lazarus: 0.24
Chama coralloides: 0.16,0.17

CARDITACEA
Cardium edule: 0.18

CRASSATELLACEA
Astarte sulcata: 0.18
Eucrassatella kingicola: 0.21,0.31,0.3,0.21,0.21,0.31

TELLINACEA
Asaphis coccinea: 0.12
Scrobicularia plana: 0.22,0.24,0.19,0.21,0.21,0.16,0.21
Soletellina nitida: 0.08,0.1

ARCTICAEA
Artctica islandica: 0.19,0.21,0.17,0.17,0.17,0.16,0.16,0.13,0.19,0.12,0.16,0.17
Coralliophaga coralliophaga: 0.11,0.13,0.13,0.13,0.13,0.18
Gaimardia trapezoides: 0.12
Glossus humanus: 0.21,0.13,0.12,0.11,0.13,0.20

VENERACEA
Anomalocardia flexuosa: 0.15

Callista chione: 0.2,0.18,0.17,0.2,0.15
Callista lilacna: 0.2,0.16
Dosinia australis: 0.21,0.22,0.17
Dosinia caerula: 0.18
Dosinia exoleta: 0.13,0.2,0.19,0.16,0.2,0.14,0.17,0.18,0.17
Dosinia prostrata: 0.14
Gemma: 0.22
Meretrix: 0.21,0.22,0.18
Paphia textile: 0.13,0.17,0.18
Periglypta puera: 0.17
Periglypta reticulata: 0.12,0.18
Pitarf fulminata: 0.16
Tapes virgenea: 0.6
Saxidomus nutalli: 0.17
Sunetta meroe: 0.15,0.15,0.1,0.16
Venerupis sp.: 0.19
Venus mercenaria: 0.16, 0.17
Venus striatula: 0.17,0.15,0.14,0.17,0.16,0.12,0.18
Venus verucosa: 0.16
Venus nux: 0.2

MYACEA
Mya arenaria: 0.09,0.13,0.1,0.1,0.12,0.15
Mya truncata: 0.14,0.14,0.08,0.1

PANDORACEA
Cleidothaerus albida: 0.17
Cleidothaerus maorianus: 0.24,0.35,02,0.24,0.38
Myadora striata: 0.3,0.3,0.25,0.25,0.27,0.23,0.26,0.22,0.26,0.25,0.2,0.26,0.21,0.23,0.22
Myadora rotunda: 0.3
Myochama anomioides: 0.22
Myochama inaequivalvis: 0.41,0.42,0.44,0.35,0.31,0.33
Myochama panderiformis: 0.21,0.22,0.23
Myochama strangei: 0.18,0.15
Myochama transversa: 0.21,0.13,0.19,0.16,0.23,0.19,0.19
Magaritacea: 0.35
Thracia convexa: 0.06,0.04
Thracia pubescens: 0.1,0.1,0.09

CORBICULACEA
Corbicula fluvialis: 0.2
Pisidium: 0.19,0.19

ANOMIACEA
Anomia ephippium: 0.36,0.40,0.4,0.39
Monia squama: 0.41,0.51,0.46

PART II: PALAEONTOLOGICAL DATA

PLICATULACEA
Jurassic
Liassic
P.gibbosa; 0.24
P. laevigata: 0.36,0.23
P.pectinoides:0.27,0.27,0.27
P.rarispina: 0.29,0.27,0.23
P.spinosa 0.22,0.2, 0.28,0.25,0.24

Upper Oxfordian
P.peregmatus: 0.28
Portlandian

P.damoni: 0.20,0.2,0.23

Cretaceous
Albian
P.sp.: 0.19,0.24
Senonian
P.osteriodes: 0.25
Santonian
P.ferryi: 0.24

Eocene
P. filamentosa: 0.27,0.24,0.28,0.17,0.23,0.18
P.mantelli: 0.25, 0.25, 0.26,0.29
P.sp: 0.21,0.16,0.28,0.26

Miocene
P.marginata: 0.14,0.14

Plio/Pleistocene
P. ramosa:0.15

Quaternary
P. sp.: 0.13,0.13

SPONDYLIDAE

Cretaceous
Campanian (Ivö Klack collection, DCM): 0.16,0.32,0.2,0.11

Palaeocene
Danian (Faxe collection, DCM): 0.25

Eocene
Upper Bracklesham beds: 0.33

Oligocene
0.27,0.26,0.22

Miocene
Burdigalian 0.26
Stage unspecified 0.22,0.24,0.22,0.25,0.22

Pliocene
0.25,0.25,0.31,0.28,0.25

Holocene
0.26

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